Modelling the population dynamics of a benthic octopus species: exploring the potential impact of environment variation and climate change

by

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Frontispiece: fractal

“Electric octopus”

by Dzeni

Declarations

Statement of originality

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Abstract

Cephalopods are increasingly targeted by fisheries, yet their population dynamics are generally poorly understood due to their intrinsically complex nature and their great sensitivity to environmental factors. As a consequence, population structure and biomass can change rapidly over short time-scales, with currently no means of predicting future recruitment or the consequences of climate change on these species. The aim of this study was therefore to develop a mechanistic model to predict the population dynamics and the potential impact of environmental variability and climate change on a cephalopod species.

The benthic octopus *Octopus pallidus* was the main focus of this research and laboratory rearing of juveniles allowed the relationships between early growth and the significant factors affecting growth to be examined (i.e. food intake, food conversion and fluctuating environmental temperatures). Results indicated high intra- and inter-individual variability in feeding rates, conversion rates and growth rates, with no indication of periodicity for any of the variables. Based on the concept that growth is bi-phasic (a rapid exponential growth phase followed by a second slower growth phase) and using results from captive studies on *O. pallidus* and *Octopus ocellatus*, a temperature-dependent bioenergetic model describing growth in octopus was developed. Model projections were consistent with laboratory data and sensitivity analyses suggested that metabolic rate has the greatest influence

on the growth threshold at which the switch from fast to slower growth occurs. In order to simulate juvenile growth trajectories in the wild, the bioenergetic model was further developed to include dynamic seasonal temperatures and individual variability in growth and hatching size. Results indicated that hatching size was secondary to inherent variation in growth rates in explaining size-at-age-differences, and that size-at-age distributions in some cohorts tended to become bimodal under certain food intake levels. Predictions from the individual-based bioenergetic models were integrated into a matrix population model, which was used to project the population under the predicted temperature conditions generated by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) from the emission scenarios of the Intergovernmental Panel for Climate Change (IPCC). Simulations suggested that increasing water temperatures might not be as beneficial to octopus as previously thought. Survivorship and incubation time were found to drive the population dynamics and while *O. pallidus* has the potential to survive under climate change conditions, the population structure and dynamics are likely to change substantially with a potential decrease in average generation time, a streamlining of the life cycle, and a possible loss of resilience to catastrophic events.

Mechanistic models relating cephalopod biology to the environment, like the one presented in this thesis, constitute a valuable way forward to elucidate population dynamics in these highly plastic animals.

Statement of co-authorship

Chapters 2-4 of this thesis have been prepared as scientific manuscripts as identified on the title page for each chapter. In all cases experimental design and implementation of the research program, modeling, data analysis, interpretation of results and manuscript preparation were the primary responsibility of the candidate, but were carried out in consultation with supervisors, and with the assistance of co-workers. Contributions of co-authors and co-workers are outlined below:

Chapter 2:

• Dr Gretta Pecl (Tasmanian Aquaculture and Fisheries Institute (TAFI)) is the primary supervisor for this PhD and provided advice on the experimental design and analyses of the results, as well as manuscript preparation.

• Dr Jayson Semmens (TAFI) is a supervisor for this PhD and provided advice on the biology of *Octopus pallidus*, as well as the experimental design and maintenance of octopus for the laboratory experiment and manuscript preparation.

• Dr Eric Grist (UHI Millenium Institute) is a supervisor for this PhD and provided advice on the statistical analyses of the results and manuscript preparation.

Chapter 3:

• Dr Eric Grist (UHI Millenium Institute) provided advice on the modeling approach, data analyses and interpretation of results as well as manuscript preparation.

• Dr Gretta Pecl (TAFI) provided advice on cephalopod biology and physiology, and manuscript preparation.

• Dr Jayson Semmens (TAFI) provided guidance on octopus biology, specifically on octopus growth, and manuscript preparation.

• Prof Susumu Segawa (Tokyo Univeristy of Marine Science and Technology) is a collaborator and provided the experimental data sets for *Octopus ocellatus*

Chapter 4:

• Dr Gretta Pecl (TAFI) provided guidance in the areas of cephalopod biology and ecology, as well as interpretation of the results and manuscript preparation.

• Dr Eric Grist (UHI Millenium Institute) provided advice on the modeling approach and manuscript preparation.

• Dr Jayson Semmens (TAFI) provided advice on the interpretation of the results and manuscript preparation.

• Prof Malcolm Haddon (CSIRO) is a supervisor for this PhD and provided advice on modeling aspects and statistical analyses and manuscript preparation.

• Stephen Leporati (TAFI) is a collaborator and provided the size-at-age datasets for wild *Octopus pallidus.*

Chapter 5:

• Prof Malcolm Haddon (CSIRO) provided guidance on the modeling approach and statistical interpretation of the results, as well as manuscript preparation.

• Dr Gretta Pecl (TAFI) provided advice in the areas of cephalopod biology and ecology, specifically on possible implications of climate change, as well as manuscript preparation.

• Stephen Leporati (TAFI) provided the fecundity dataset for wild *Octopus pallidus.*

• Dr Alistair Hobday (CSIRO) provided the water temperature predictions for the Tasmanian region under the climate change scenario A1FI.

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I would like to thank my family, for their enduring love, for never doubting me and supporting me throughout the years. A special thanks to the two men in my life: my partner, Peter-Johannes Pfeiffer, and my son, Niels. We have come a long way, sailed through the stormy waters and pulled through stronger. You have brought out the best (and sometimes the worst…) in me. Weil I eich mog.

And finally, I would like to share this haiku about the art of biological modelling, written in a moment of disillusionment:

Sometimes they work fine

Yet most times they crap themselves

Models are like that…

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General Introduction

CEPHALOPODS: ROLE AND CHARACTERISTICS

Cephalopods are important ecological components of marine food webs as they are both significant prey items, consumed by a variety of large fishes, birds and marine mammals (Clarke 1996; Croxall and Prince 1996; Klages 1996; Smale 1996; Santos et al. 2001), and voracious, opportunistic predators feeding on a vast array of fishes and crustaceans (Rodhouse and Nigmatullin 1996). In addition, squids, octopuses and cuttlefishes are a valuable human food source. With the depletion of many fish stocks and the consequent global decline in traditional finfish catches, cephalopods stocks are increasingly being exploited (Caddy and Rodhouse 1998; Jackson and O'Dor 2001). As a result, since the 1950's, total landings of cephalopods have increased steadily, reaching 3 to 4 million tonnes annually over the last decade (Fig. 1.1) (FAO 2005). These figures are likely to be under-estimates, however, with the real values substantially higher as many coastal human populations derive a significant proportion of their protein intake from locally caught cephalopod species, and the landings from these artisanal fisheries are generally unrecorded and unquantified (Boyle and Rodhouse 2005).

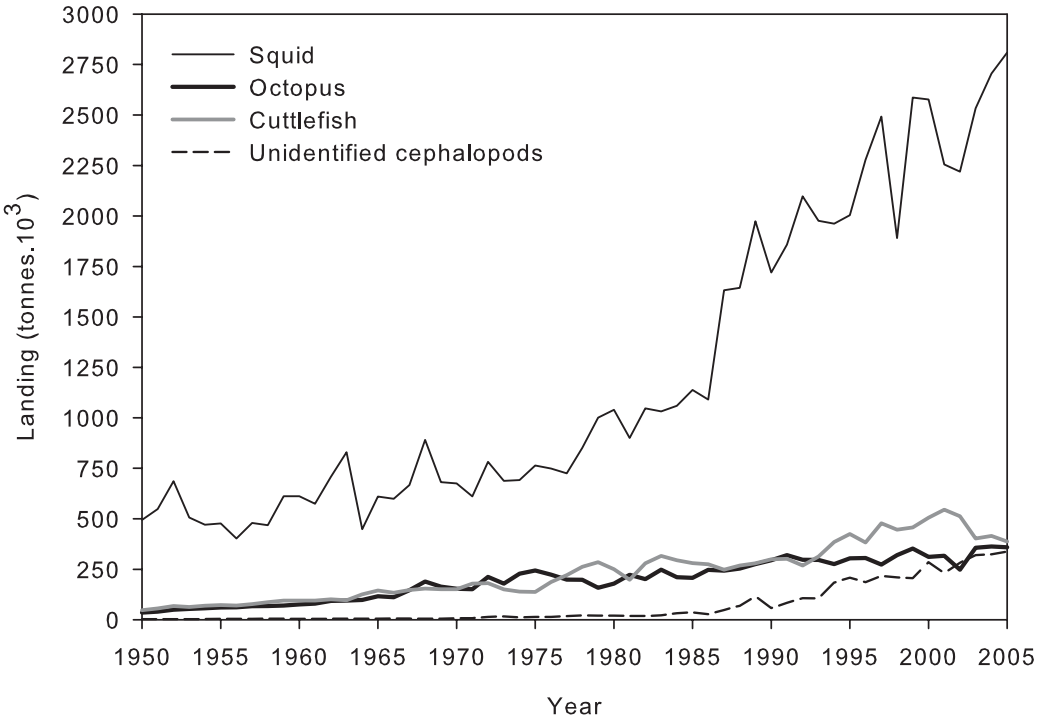

Fig. 1.1 Global landing of cephalopods from 1950 to 2005. Data include commercial, industrial, recreational and subsistence purpose catches (sourced from the FAO Global Production Statistics).

Cephalopods differ significantly from fish in their biology and physiology (O'Dor and Webber 1986). Finfish are typically long-lived and iteroparous while cephalopods, with the exception of nautiluses and deep-sea species, are characterized by short life-spans (<2 years) and reproduction constrained within a single breeding season (Boyle and von Boletzky 1996). Coleoid cephalopod growth (i.e. squid, cuttlefish and octopus) is also rapid and continuous (Moltschaniwskyj 2004), as opposed to the typically asymptotic growth observed in fish. While it is generally accepted that cephalopod growth is non-asymptotic, the specific shape of the growth

curve is still subject to considerable debate. A variety of models have been fitted to growth data, including power, linear, exponential, sigmoidal, part parabolic and cyclic (see Semmens et al. 2004; and Arkhipkin and Roa-Ureta 2005 for a review). Although it is yet to be demonstrated for wild animals, studies have shown that individuals reared in captivity generally exhibit two-phase growth consisting of an initial rapid exponential phase followed by a slower second power growth phase close to linear, which ends abruptly at the end of the life cycle (DeRusha et al. 1987; Forsythe and Hanlon 1988; Forsythe and Hanlon 1989; Forsythe et al. 2001b; Segawa and Nomoto 2002). In some species, the slower growth phase is better represented by an exponential (Hatfield et al. 2001; Hoyle 2002) or true logarithmic (Cortez et al. 1999a; Ribgy 2004) model.

PLASTICITY AND POPULATION DYNAMICS

In addition to inter-specific differences in growth pattern, cephalopods exhibit high intra-specific plasticity, not only in growth but in many life history traits. Much of this variability relates to the strong influence of environmental factors, particularly temperature and food availibility, on all aspects of their life cycle (Forsythe and Van Heukelem 1987; Boyle and vonBoletzky 1996; Forsythe et al. 2001a; Vidal et al. 2002). Temperature and maternal food ration can have antagonistic effects on hatchling size, with low temperatures producing larger hatchlings due to longer incubation times (Boletzky 1994) while poorly fed females produce smaller

hatchlings due to lower yolk reserves in the eggs (e.g *Euprymna tasmanica*, Steer et al. 2004). Low temperatures or under-nutrition early in the life cycle can result in slow growth (Segawa 1990; Hatfield et al. 2001; Jackson and Moltschaniwskyj 2002; Segawa and Nomoto 2002; Semmens et al. 2004) and/or delayed maturity (Forsythe and Hanlon 1988; Forsythe et al. 2001b), with these factors resulting in larger adult size and longer life spans (Jackson 2004). Under-nutrition or low food availability during the later phases of the life cycle however can induce cephalopods to reproduce earlier at smaller sizes (Mangold 1987).

Another factor that may partly explain variation between siblings is multiple paternity (e.g. squids, Shaw and Boyle 1997; Buresch et al. 2001; cuttlefish, Naud et al. 2004), although the high levels of individual plasticity of cephalopods are unlikely to have a strong genetic basis as levels of genetic variation are typically relatively low in this group (Shaw et al. 1999). Instead, the variability observed is more likely to be influenced by phenotypic plasticity, where a single genotype is capable of producing different phenotypes as a result of environmental conditions (Boyle and von Boletzky 1996). As a consequence of strong sensitivity to environmental factors, high turnover of generations and the high levels of individual variability in life history parameters, the population dynamics of cephalopods are difficult to unravel as population structure and

biomass change very rapidly over short time scales (Grist and des Clers 1998).

Much of our understanding of cephalopod growth, maturation, physiology and energetics is derived from controlled laboratory studies. Although these are essential and have been invaluable in assessing the impact of environmental factors on cephalopod life history, they do not necessary reflect the conditions experienced by individuals in the wild. Despite the major impact of temperature on cephalopod life history, with the exception of Leporati et al. (2007) and Hoyle (2002), captive experiments have only used fixed temperature regimes to investigate the impact of temperature on life history characteristics of cephalopods, and there is little information regarding the impact of dynamic temperatures, as would be experienced in nature.

As for many marine species, field data are difficult to obtain and often limited to the portion of the population that is exploited. In the case of cephalopods, data on juveniles are typically scarce as immature animals often do not recruit to the fisheries due to size-selective gear and/or spatial segregation of life history stages (i.e. division between nursery and spawning grounds). Moreover, animals in the very early portion of the life history are often inconspicuous and their locations generally remain unknown. Consequently, crucial data such as juvenile growth rates or

feeding rates in the wild are generally lacking. This knowledge gap undermines our understanding of the underlying mechanisms driving and regulating population dynamics in these species. This is a major problem for fisheries management because of the limited information for forecasting future recruitment (Rodhouse 2001). Given the absence of generational overlap in most cephalopod species, population size and structure is a direct function of the success of breeding and recruitment from the previous year (Caddy 1983), rendering populations very vulnerable due to the lack of enduring age classes to buffer against stock collapse (Steer et al. 2007). Currently, predictions of recruitment strength are restricted to some species of squids and cuttlefish and involve correlating paralarval densities from structured surveys to the following year's stock *(e.g. Loligo opalescens*, Zeidberg et al. 2006) or assessing population density offshore two to six months before animals move inshore to the fishing grounds for spawning (e.g. *Illex illecebrosus*, Dawe and Warren 1993; *Loligo forbesi*, Pierce et al. 1998; *Sepioteuthis australis*, Steer et al. 2007). Other approaches being investigated include relating population abundance to environmental factors such as sea surface temperatures (SST) or annual environmental indices (e.g. North Atlantic oscillation index) at particular times of the year (Bellido et al. 2001; Pierce and Boyle 2003; Chen et al. 2006; Lefkaditou et al. 2008; see Pierce et al. 2008 for a review). However, the strength of these predictions is highly

variable and any improvement in our understanding of environmental impact on cephalopod early life history in the wild would be beneficial.

CEPHALOPODS AND CLIMATE CHANGE

While the lack of in-depth understanding of the mechanisms driving population dynamics and recruitment is a concern in the shorter term for the management of stocks, it is especially problematic when attempting to predict the future of cephalopod populations with regards to global climate change. There are many uncertainties surrounding the impacts of climate change on marine ecosystems, many of which are linked to our incomplete understanding of marine carbon-cycling and ocean-atmosphere circulation mechanisms (Mann and Lazier 2006). Changes will nevertheless occur, one of the most definite being an increase in temperature. By the end of the century, the global ocean temperature is predicted to rise between 1.8°C and 6.4°C depending on future carbon emission scenarios, with an average of 4°C under the highest emission scenario (namely A1FI, IPCC 2007). The various models agree that the maximum warming will occur in the high latitudes of the northern hemisphere, mainly due to melting ice and changing surface albedo (reflectivity of sun's radiation), whereas the minimum is expected in the Southern Ocean, due to ocean heat uptake. However, generalisation is difficult as regional differences exist because of localised atmospheric and oceanographic features. For example, while sea surface temperatures (SST) are expected to increase by 2.5°C to 2.8°C in the Southern Tasman Sea by

2070 under the A1FI scenario (CSIRO 2007), coastal water temperatures in Tasmania are expected to rise, in the same time period, between 1.4°C to 4.1°C due to Tasmania's complex current system.

As cephalopods adapt rapidly to varying environments and appear to thrive in warmer conditions due to accelerated growth and their opportunistic nature, it has been suggested that cephalopods will prosper with climate change, providing there is sufficient food availability (Bildstein 2002). However, higher temperatures also lead to smaller hatchlings and potentially smaller adults (Pecl et al. 2004b), implying that hatchling size and post-hatching growth rate will likely be opposing forces acting on the size at age of adult cephalopods (Pecl and Jackson 2008). As temperature also has a direct effect on cephalopod metabolism, as well as that of their prey and predators, climate change is certain to have consequences for species abundance and activity rates (Bailey and Houde 1989).

Rising ocean temperatures are only one of the many consequences of global warming. Levels of atmospheric CO_2 are expected to rise, increasing the quantity of CO_2 that permeates the surface mixed layer of the oceans and resulting in an estimated drop in pH of 0.14 to 0.35 units by 2100 (IPCC 2007). At present, the natural variation of seawater pH throughout the world's oceans is 7.5 to 8.3 (Seibel and Fabry 2003) so

ocean acidification could result in a pH range of 7.15 to 7.95 under the highest emission scenario. In cephalopods, oxygen binding and blood transport is extremely sensitive to changes in pH (Miller and Mangum 1988; Pörtner et al. 2004). Therefore the acidification of oceanic waters is likely to limit oxygen uptake in many species, with consequences for activity rates, growth, reproduction and survival (Seibel and Fabry 2003; Rosa and Seibel 2008). Due to their high rates of activity and elevated metabolism, squids are more likely to be affected than octopus and cuttlefishes (Zielinski et al. 2001), whose blood oxygenation only becomes markedly affected at a water pH<7.4 (*Sepia officinalis*, Zielinski et al. 2001) and pH<7.2 (*Octopus dofleini*, Miller and Mangum 1988) respectively against pH<7.5 for squids *(Illex illecebrosus*, Pörtner and Reipschläger 1996).

The predicted increases in precipitation and freshwater runoff are likely to decrease salinity in some areas, which would affect incubation and embryonic development (Paulij et al. 1990; Cinti et al. 2004; Sen 2005) as well as adult survival (Chapela et al. 2006). Increased turbidity could also affect species with ritualised mating behaviour based on sight, reducing breeding success as observed in *Loligo vulgaris reynaudii* (Roberts and Sauer 1994; Roberts 1998; Rodhouse 2001). The potential increase in the incidence of severe weather and more common and intense El Niño events (Easterling et al. 2000) is also likely to affect the population structure of cephalopod species, as has occurred during past El Niño/La Niña events

(Arntz et al. 1988; Jackson and Domeier 2003; Ish et al. 2004; Zeidberg et al. 2006; Chen et al. 2007).

Other predicted consequences of climate change include modification of the patterns of ocean stratification and/or deep-ocean circulation, changes in the productivity and location of upwelling areas, as well as in the intensity of many currents (Mann and Lazier 2006), which would have consequences for nutrient availability and the distribution of migratory species and those with planktonic stages (paralarvae). Climate change will also bring about modifications in biogeography, as poleward shifts in the range of many species are expected. Such migrations to more suitable thermal environments have already taken place, with the appearance of subtropical and tropical species in temperate areas, such as the observations of the squid *Alloteuthis africana* and the common paper nautilus *Argonauta argo* in Spanish waters (Guerra et al. 2002). For completely benthic species, which include some octopus and cuttlefishes, the lack of larval dispersion by means of currents and the limited movement capacities of adults might prove problematic under changing temperature conditions, and animals may be forced to undergo shifts in their depth distribution to match their thermal preferences.

Given the complexity and the potential cascading effects of climate change, predicting the future for particular cephalopod populations is challenging and has not yet been attempted, mostly because the crucial understanding

of population dynamics that is required to make predictions is lacking for most cephalopod species. Importantly, understanding population dynamics requires a sound knowledge of the characteristics of the individuals constituting the population (Vanoverbeke 2008), in particular the mechanisms dictating individual growth and how biotic and abiotic factors influence developmental and reproductive processes in the wild. This knowledge is currently lacking and is the focus of the present research.

AIMS AND THESIS STRUCTURE

The ultimate aim of this study is to predict the potential impact of climate change on a cephalopod population with limited dispersal capacity. This is achieved by firstly exploring the early life-history processes in juvenile octopus, and subsequently developing bioenergetic models describing growth and maturation as a function of the main biotic (size, individual variability, nutrition) and abiotic (environmental temperature) factors influencing cephalopod life history. Finally, the population is projected through to 2070 according to the climate predictions of the International Panel for Climate Change (IPCC 2007).

The western Bass Strait population of *Octopus pallidus* was selected for this study due to the holobenthic lifestyle of the species, the physical location of the population on a continental shelf with limited possibility of vertical migration (Fig. 1.2), and the commercial value of the stock. Data for a

second holobenthic octopus, *Octopus ocellatus*, were also used to validate the basic bioenergetic model.

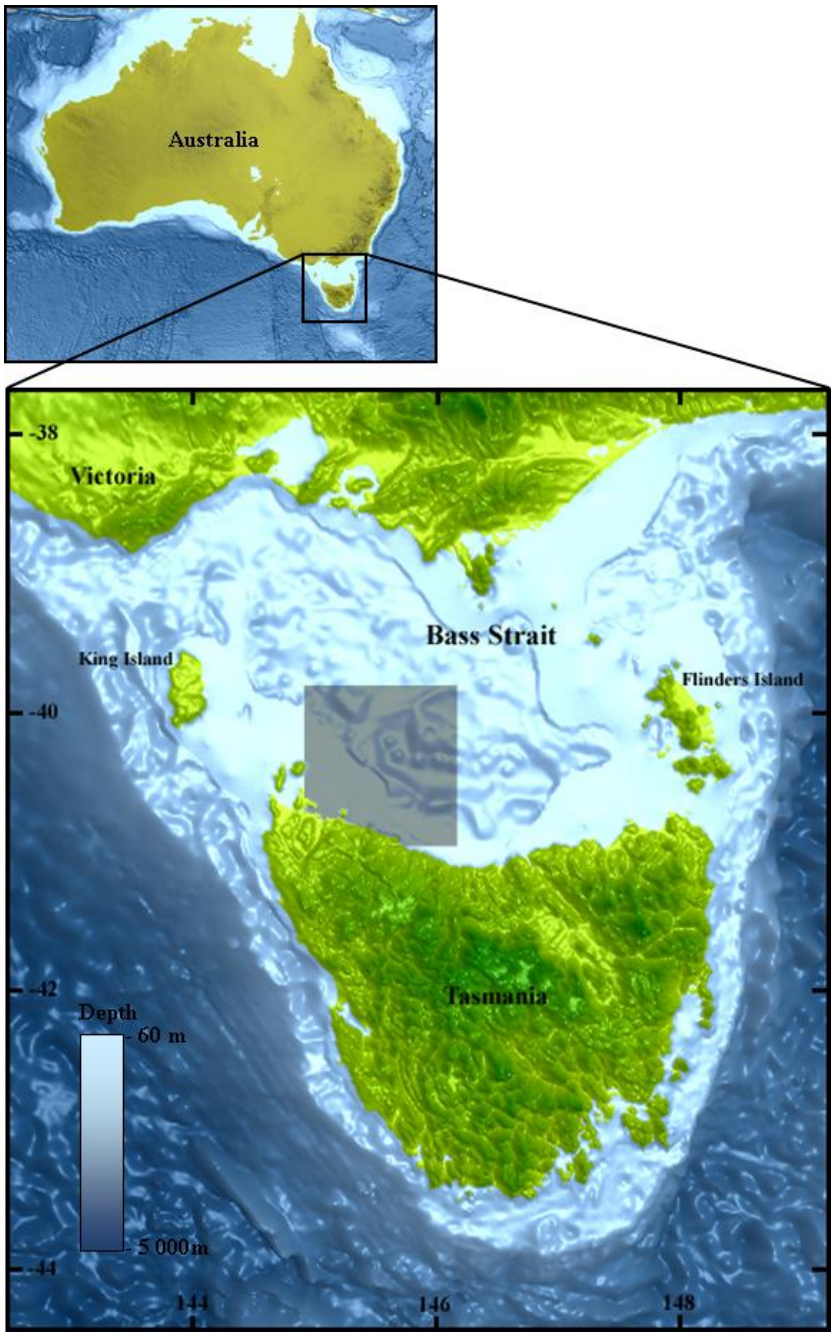

Fig. 1.2 Map of the study area. The grey square represents the location of the *O. pallidus* population from this study.

The thesis is organized into four data chapters (2-5) culminating in a general discussion (chapter 6). The primary aims and topics addressed in each of the data chapters are as follows:

Chapter 2: The early life-history processes: relationships between temperature, feeding, food conversion, and growth

This chapter explores the early-life history of *Octopus pallidus* through a captive experiment. Since initial growth is exponential, early life-history is critical in determining future growth trajectories. The specific aim was to investigate, at the individual level, the relationship between early growth and the significant factors affecting growth, namely food intake, food conversion and fluctuating environmental temperatures. The feeding and growth data collected in this chapter form the basis on which the bioenergetic models developed in the following two chapters were built.

This research is published in: *Journal of Experimental Marine Biology and Ecology* (2008) 354: 81-92 (see Appendix).

Chapter 3: Modelling the impact of temperature on the growth pattern of octopus using bioenergetics

In this chapter, a bioenergetic model describing growth is developed. Based on the concept that growth is bi-phasic (initial rapid exponential growth shifting to a slower growth rate), a temperature-dependent model which incorporates the energy balance between food intake and expenditure in growth and metabolism is tested on *Octopus ocellatus* and

Octopus pallidus growth data in captivity. The model is then employed to investigate growth patterns occurring at different fixed temperatures for both species.

This research is published in: *Marine Ecology Progress Series* (2009) 374: 167-179 (see Appendix).

Chapter 4: Modelling size-at-age in wild immature animals: the relative influence of the principal abiotic and biotic factors

This chapter explores the predicted growth of *Octopus pallidus* in the wild. The bioenergetics model developed in the previous chapter was modified to include dynamic seasonal temperatures and individual variability in growth and hatchling size, in order to simulate the juvenile growth trajectories of individuals hatched in different seasons. This allows the investigation of the relative influence of the principal biotic (hatchling size, individual variability, nutrition) and abiotic (environmental temperature) factors affecting size-at-age in wild immature *Octopus pallidus*.

This research is published in: *Marine Ecology Progress Series* (2009) 384: 159-174 (see Appendix)

Chapter 5: Potential impact of climate change on the Eastern Bass Strait pale octopus population

In this final data chapter, the western Bass Strait *Octopus pallidus* population is projected from present time to 2070, and the impact of predicted sea temperature changes (from a high emission scenario) on the

population structure and dynamics is assessed. This is achieved by integrating the results of the individual-based bioenergetic models described previously into a complete matrix population model, therefore accounting for the effect of environmental temperature and individual variability on the biology of *O. pallidus* (e.g. egg incubation time, growth, reproduction).

STUDY SPECIES

This study focuses on two commercially exploited benthic octopus species, *Octopus pallidus* and *Octopus ocellatus*, with the former being the main focus of the research. Both species belong to the family Octopodidae and are characterized by holobenthic hatchlings as opposed to other larger merobenthic octopus species with planktonic young (paralarvae).

Octopus pallidus (Hoyle 1885)

Commonly known as the pale octopus, *Octopus pallidus* is a medium sized benthic octopus reaching up to 1.2 kg with an estimated life span of 12 to 18 months (Leporati et al. 2008b). Endemic to the temperate waters of south-east Australia (Fig. 1.3), pale octopus are found on sand and mud habitats from shallow waters to depths of almost 600m (Norman 2000). Females lay around 150-270 large eggs (11-13 mm length) that are attached singly to the roof of crevices or any sheltered substratum (Stranks 1988; Stranks 1996; Norman 2000). Hatchlings are well developed and settle immediately in the benthos, begining to forage shortly after hatching

(Norman and Reid 2000). Populations of this species show very little overlap in generations despite all year round egg-deposition (Leporati et al. 2008b). This species is targeted recreationally throughout its range and commercially in northern Tasmanian waters (Bass Strait region), with catches of 81 tonnes in 2007 (Leporati et al. 2008a).

Octopus ocellatus (Gray 1849)

The gold-spot octopus *Octopus ocellatus* is a small benthic octopus (less than 100g) with a life span of 6 to 12 months depending on geographical location (Segawa and Nomoto 2002). Gold-spot octopus inhabit the shallow waters from the southern coast of Hokkaido to the Chinese continent and southern Korean Peninsula (Okutani et al. 1987), preferring sandy and muddy habitats (Fig. 1.3). Female *O. ocellatus* lay 300 to 400 large eggs (7 mm length) in crevices and empty shells, which develop into benthic hatchlings (Yamoto 1941a; Yamoto 1941b). The gold-spot octopus is important in both commercial and recreational fisheries along the Japanese coast especially in Tokyo Bay and the Seto Inland Sea (Segawa and Nomoto 2002).

ANIMAL ETHICS

All research conducted throughout this thesis complied with the guidelines of and was approved by the Animal Ethics Committee of the University of Tasmania under projects No. A0008385 and A0008130.

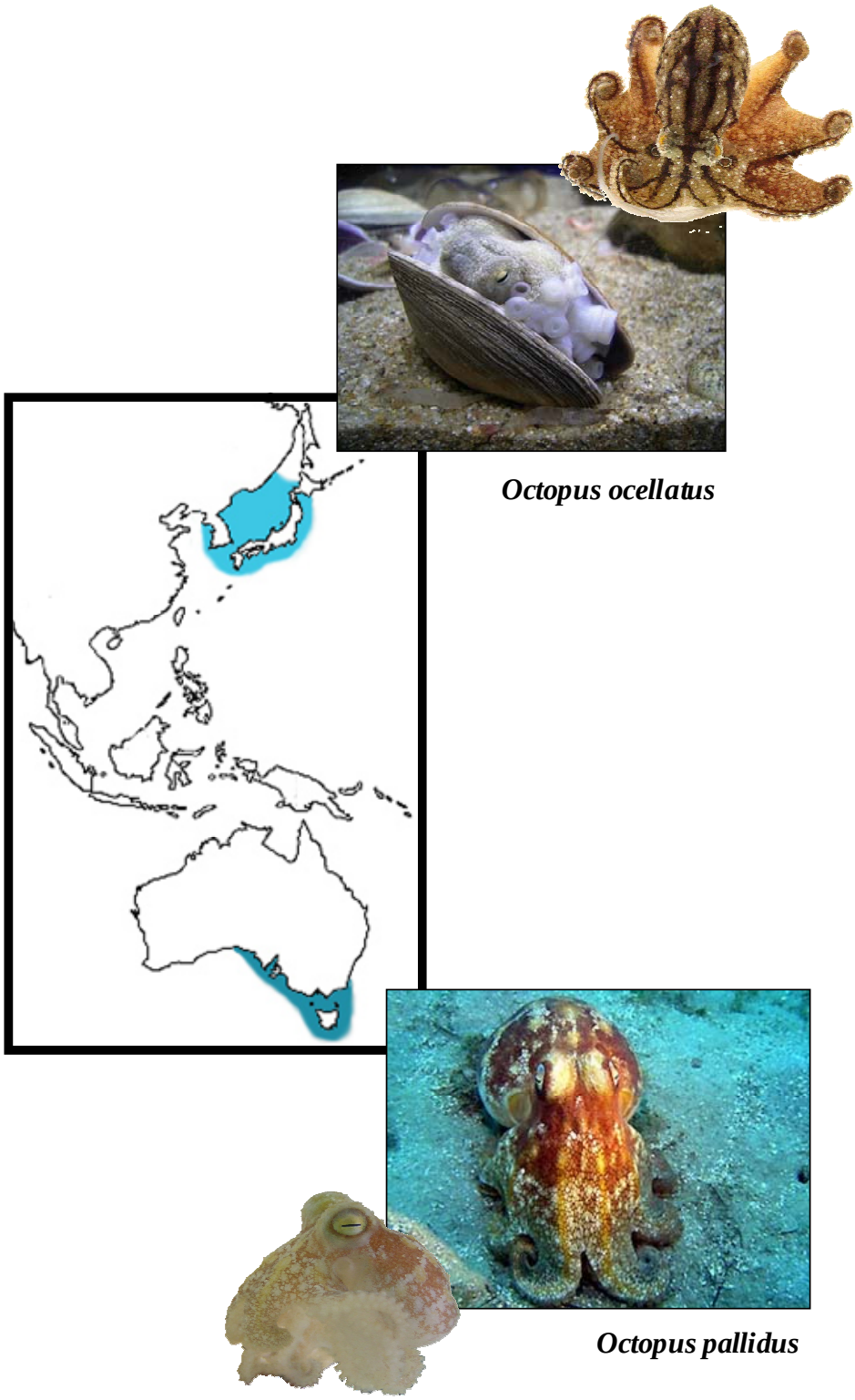

Fig. 1.3. Distribution of pale octopus *Octopus pallidus* and gold-spot octopus *Octopus ocellatus*. Photos courtesy of Kobe Municipal Suma Seaside Aquarium and Kay (*O. ocellatus*), and Harry Wright (adult *O. pallidus*

Ch 2

The early life-history processes: relationships between temperature, feeding, food conversion and growth

This Chapter previously published as:

André J, Pecl GT, Semmens JM and Grist EPM (2007) Early life-history processes in benthic octopus: relationships between temperature, feeding, food conversion, and growth in juvenile *Octopus pallidus*. Journal of Experimental Marine Biology and Ecology 354: 81-92

ABSTRACT

Initial growth in octopus is exponential, making early life-history critical in determining growth trajectories. Few captive studies have however examined the early life history of cephalopods in fluctuating temperatures as would be encountered in the wild. This chapter investigates the relationship between early growth and the significant factors affecting growth, namely food intake, food conversion and fluctuating environmental temperatures. Pale octopus hatchlings were reared in captivity under either a warming or cooling temperature regime. Individual variations and periodicity in feeding rates F_r, food conversion rates C_r, growth rates G_r, and the relationship between these variables and temperature were examined weekly. Food conversion rates were variable between individuals but also within individual octopus and animals exhibited large fluctuations in C_r during the experiment, exceeding 100%.d^{-1} in one instance. Although individual F_r, C_r and G_r displayed fluctuations over time, there was no evidence of periodicity for any of the variables. Changes in temperature were not significantly correlated to changes in F_r, C_r or G_r. Feeding rate did not appear to influence growth rate or food conversion rate. Food conversion rate was negatively correlated to feeding rate in the same week, and positively correlated to growth rate. Short periods of low or no food consumption were common and the high values obtained for food conversion rate for some individuals suggest that octopus can grow substantially with little or no food intake. The individual variability observed in octopus growth may be dependent on the growth mechanism involved, specifically a fine balance between the continuous hyperplasic and hypertrophic growth found in cephalopods.

INTRODUCTION

In common with other cephalopods, individual growth in octopus is highly variable, even within groups of siblings reared under identical conditions (Van Heukelem 1976; Forsythe and Van Heukelem 1987). Numerous biotic and abiotic factors can influence growth, including temperature (Forsythe and Hanlon 1988; Forsythe 1993; Pecl 2004), food quality and quantity, age, size, gender, stage of maturity and level of activity (Forsythe and Van Heukelem 1987). In the juvenile phase, temperature (Forsythe and Van Heukelem 1987), food ration (Villanueva et al. 2002), food quality (Villanueva 1994) and hatchling size (Leporati et al. 2007) appear to have the most significant impact on growth. Higher temperatures result in higher growth rates for octopus with both benthic (Forsythe and Hanlon 1988; Segawa and Nomoto 2002) and planktonic (Itami et al. 1963; Villanueva 1995) hatchlings, as well as for deep-sea octopus (Wood 2000). However, most studies have only used one or several fixed temperature regimes to investigate the impact of temperature on growth, with only Leporati et al. (2007) having explored the effect of seasonal temperatures on the growth of octopus hatchlings. There is in general little information regarding the impact of dynamic temperatures, as would be expected in nature, on the physiology of cephalopods.

Variability in individual food conversion may also contribute to differences in individual growth rates. Food conversion (or gross growth

efficiency) is highly variable between individuals even for octopus reared on the same diet (Mangold and von Boletzky 1973). High levels of activity, low food intake (Wells and Clarke 1996) and sexual maturity (Mangold 1983a; Mangold 1983c; Klaich et al. 2006) are known to lower food conversion since less energy is available for somatic growth. Food conversion, however, appears independent of sex (Hanlon 1983; Forsythe 1984) and body size (Mangold 1983a). It also appears independent of temperature in some species (*Octopus vulgaris*, Mangold and von Boletzky 1973; *Eledone moschata*, Mangold 1983a), but not in others (*Octopus tehuelchus*, Klaich et al. 2006). Gross growth efficiency (food conversion rate) appears variable at the individual level, exhibiting apparent periodic fluctuation over time in some species (Mangold and von Boletzky 1973; Mangold 1983a; Mangold 1983c) although the cause of these fluctuations has not been established.

The objective of this chapter was to examine the relationship between growth in juvenile octopus and significant factors affecting growth, namely food intake, food conversion and temperature. Individual feeding rate, food conversion rate, and growth rate were determined for pale octopus hatchlings reared under identical nutritional conditions but two different dynamic temperature regimes. As octopus initially grow exponentially, the early life-history is critical in determining their growth trajectory and there has been very little focus on this aspect of their life

cycle, except in a few commercial species (Segawa and Nomoto 2002; Iglesias et al. 2004). This chapter aims to improve the current understanding of the growth processes in juvenile octopus.

MATERIAL AND METHODS

Study animals and experimental design

Two brooding females (designated as females A and B) were collected in March 2005 from the commercial pot fishery in north-west Tasmania, Australia (40° 49.268; 145° 39.774 west and 40° 50.240; 145° 42.091 east, 45 meters depth). Animals were maintained in separate 250 litre tanks in an indoor system at ambient sea temperature (22−11°C from March to July) until the eggs hatched. The first hatching occurred 123 days after collection.

After an acclimatisation period of 24 hours, hatchlings were placed in individual two litre containers fitted with mesh sides to allow water flow and a scallop shell for shelter. The containers were kept in 250 l stock tanks under a fluorescent lighting regime which replicated natural daylight variation (06.00−18.00 hrs light, 18.00−06.00 hrs dark). Two temperature regimes were established: a warmer temperature regime (increasing from 16°C to 18°C over a period of 36 days then stable at 18°C for 107 days) and a cooler temperature regime (decreasing from 16°C to

14°C over a period of 36 days then stable at 14°C for 107 days). Temperature was altered by 1°C on day 18 and day 36 of the experiment (Fig. 2.1), and temperature in the tanks was recorded every 15 mins by two data-loggers (StowAway Tidbit, USA, http://www.onsetcomp.com).

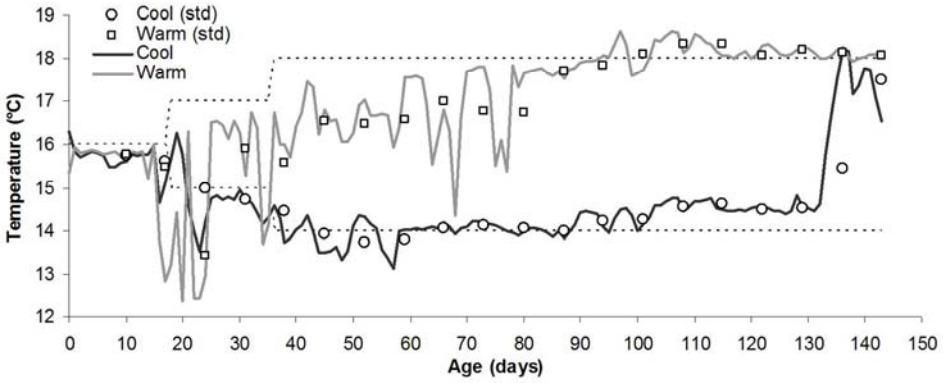

Fig. 2.1 Intended (---) and actual (—) temperature regimes recorded during the experiment. Standardised (std) temperature used in the time series analysis (see Data analysis section p. 28)are represented by circles for the cool regime and squares for the warm regime.

Four randomly selected day-old hatchlings (two from female A and two from female B all born on 19/07/05) were held under each temperature regime. Individuals were designated as octopus Cool1 to Cool4 and Warm1 to Warm4 according to their temperature regime (Table 2.1). Growth and food intake was individually monitored for a period of 143 days.

Table 2.1 Individual IDs, lineage (mother A or B), hatch weight, survival time and temperature treatment for the eight *O. pallidus* hatchlings reared in the experiment for 143 days. Warm4 was kept another 45 days beyond the experiment.

	ID	lineage	hatch weight (g)	survival (days)
Cool (16– 14°C)	Cool1	B	0.281	143
	Cool2	B	0.251	143
	Cool3	A	0.224	143
	Cool3	A	0.258	143
Warm (16– 18°C)	Warm1	B	0.263	57
	Warm2	B	0.303	143
	Warm3	A	0.235	94
	Warm4	A	0.206	188

Growth, food consumption, and food conversion rate

Individuals were weighed every 5 to 10 days and the instantaneous growth rate G_r, expressed as the percent increase in body mass per day, was calculated using the standard exponential growth formula:

$$G_r = \frac{\ln B_2 - \ln B_1}{t_2 - t_1} \times 100 \quad (1)$$

where B_1 and B_2 are body masses (g) at time t_1 and t_2 (Forsythe and Van Heukelem 1987).

To describe growth as a function of age, linear ($y = a + mx$), exponential ($y = ae^{mx}$) and power ($y = ax^m$) functions were fitted to the data sets. The

best fit model was chosen on the basis of the highest adjusted r^2 values (DeRusha et al. 1987; Hatfield et al. 2001). Adjusted r^2 values were calculated by linear regression to B versus t for the linear model, log(B) versus t for the exponential model, and log(B) versus log(t) for the power model. Average growth for each temperature treatment was calculated as the mean of individual growth equation parameter values.

All individuals were fed porcelain crabs (*Petrolisthes elongatus*) collected from around the Hobart area (Tasmania). Two live crabs, whose relative body weight totalled between 4% and 12% of the octopus body weight, were supplied daily to each animal. The level of food offered was comparable to the level of food consumed by other octopus species reared in captivity under *ad libitum* condition (Joll 1977; Mangold 1983b; O'Dor and Wells 1987). Before being fed to each individual octopus, crabs were dried with absorbing paper and weighed on a digital scale to 0.001g accuracy. Uneaten crab remains from the previous day were removed from each container and frozen immediately for later analysis. Any live uneaten crab was removed and weighed.

After defrosting, remains were washed three times with ammonium formate (0.5 M) to remove any salts before being dried in an oven for 24 hours at 60°C. The samples were then placed in a desiccator for one hour to remove any moisture and weighed on a digital scale to 0.0001g accuracy. Wet weight (ww) and dry weight (dw) in grams were obtained for 30

randomly selected samples of remains in order to calculate the ww/dw conversion factor.

The quantity of food consumed in a given day D was:

$$D = w_f - w_u - w_r \tag{2}$$

where w_f denotes the wet weight (g) of live crabs fed to the octopus, w_u denotes the wet weight (g) of any live crabs uneaten the next day and w_r denotes the wet weight (g) of remains from eaten crabs.

The weight specific feeding rate F_r expressed as a percentage of body mass per day was calculated according to Houlihan et al. (1998):

$$F_r = \frac{D_t}{B_m \times t} \times 100 \tag{3}$$

where t is the number of days between two weighings, D_t is the amount of food (g wet weight) consumed over the time interval t, and B_m is the mean body weight (g wet weight) of the octopus over the time interval t.

Food conversion (%) expresses the amount of food intake required to fuel a unit amount of growth. To explore the relationship with F_r and G_r, we have expressed food conversion C_r as a rate in percentage per day, which we calculated according to a modification of the Mangold and von Boletzky (1973) formulae:

$$C_r = \frac{\Delta B}{D_t \times t} \times 100 \tag{4}$$

where ΔB is the difference in body mass (g) between two weighings, t is the number of days between two weighings, and D_t is the amount of food (g wet weight) consumed over the time interval t.

Data analysis

For all averages given, a corrected standard error $SE^* = t \times SE$, where t is the t-score, was used where sample size was smaller than 20 (Fowler et al. 1998). Significance level throughout the analysis was set at $p < 0.05$. Time series analysis was performed on individual feeding rate F_r, growth rate G_r, food conversion rate C_r, and temperature T data. Weights were obtained every five to ten days and the resulting time series were standardised in terms of seven day time steps by the use of linear interpolation. Accordingly, F_r, G_r, C_r and T were calculated over the same time step. Time series exhibiting linear trends were detrended linearly. Time series (F_r, G_r and C_r) were first analysed separately using autocorrelation plots to assist with identifying any cycles. Since data were in weekly time steps, lag 1 corresponded to a time shift of seven days, lag 2 a time shift of 14 days and so on. Where a significant autocorrelation was established, the time series was further investigated through partial autocorrelation plots. Partial-autocorrelation measures the strength of the correlation at specific lag (e.g. lag 4) while removing the effects of all autocorrelations below that lag (i.e. autocorrelation occurring at lags 0, 1, 2 and 3). Only autocorrelation analyses that were supported by partial autocorrelation are presented. The relationships between time series T, F_r, G_r and C_r (Fig.

2.2) were examined separately using cross-correlation and partial cross-correlation analyses. Partial correlation coefficients (r) were calculated when significant correlations were established.

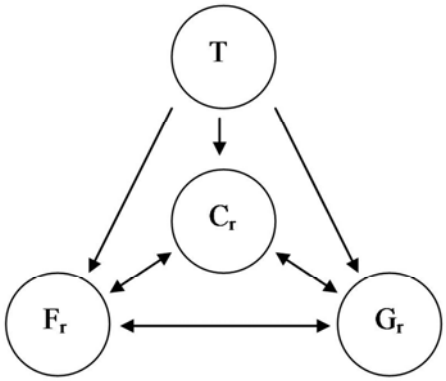

Fig. 2.2 Schematic diagram of the relationships between temperature T, feeding rate F_r, growth rate G_r and food conversion C_r investigated in this chapter.

To assess the direction of influence (e.g. if changes in x caused changes in y, or the opposite), time series x were time-shifted against y both forward (showing the effect of x on y, referred to as plots of x on y) and backward (showing the effect of y on x, referred to as plots of y on x). Given the relatively short lengths of all time series (20 data points), cross-correlations and partial cross-correlation analysis beyond a lag 6 (42 days) were considered to be redundant in view of the likelihood of type I and type II errors occurring at higher lags. The mean F_r, G_r and C_r time series were also calculated for each temperature regime and analysed as previously for individual time series. The software R version 2.2.1 was used to carry out all the analyses.

RESULTS

The mean hatch weight (g ± SE*) was 0.231 ± 0.034 for hatchlings from female A (range= 0.206 − 0.258 g, n = 4) and 0.275g ± 0.036 for hatchlings from female B (range= 0.251 − 0.303 g, n = 4). Octopus did not appear stressed (inking and jet escape movement were rarely seen) and spent most of their time sheltering under the scallop shell. Little movement was observed and so the level of activity was considered minimal. The survival rate over the durarion of the experiment was 75%, with two octopus reared under the warm treatment (Warm1 and Warm3) dying for unknown reasons at 57 and 94 days respectively after hatching. Data for these individuals were discarded in this chapter because there were too few data points to establish sufficiently long individual feeding and growth data series.

Temperatures in the two treatments fluctuated more than originally intended due to mechanical failures of the heater/chiller units (Fig. 2.1). The treatments nevertheless followed the intended main trend of increasing (warm) and decreasing (cool) temperature with time. These shorter term temperature fluctuations were an integral part of the subsequent time series analyses which were performed.

Food consumption, food conversion rate, and growth rate

All octopus started feeding within hours after hatching, preying on the smallest size crabs (2mm carapace length). Five out of the six individuals exhibited at least one subsequent period of "starvation" (ranging from 1 to 7 days) in which they did not eat and lost weight. In general, daily food consumption *D* increased with body weight. The mean *D* (g wet weight ± SE) for the warm regime was 0.024 ± 0.002 and 0.020 ± 0.001 for the cool treatment.

The mean feeding rate (% body weight per day ± SE) was 2.87 ± 0.16 for octopus reared under the warm treatment (range = 0.79 − 5.69% body weight.day^{-1}, n = 40), and 2.45 ± 0.12 for octopus reared under the cool treatment (range = 0.10 − 5.93% body weight.day^{-1}, n = 80). Although fluctuations appeared regular in these standardised time series (Fig. 2.3), autocorrelation plots revealed no significant periodicity (Fig. 2.4).

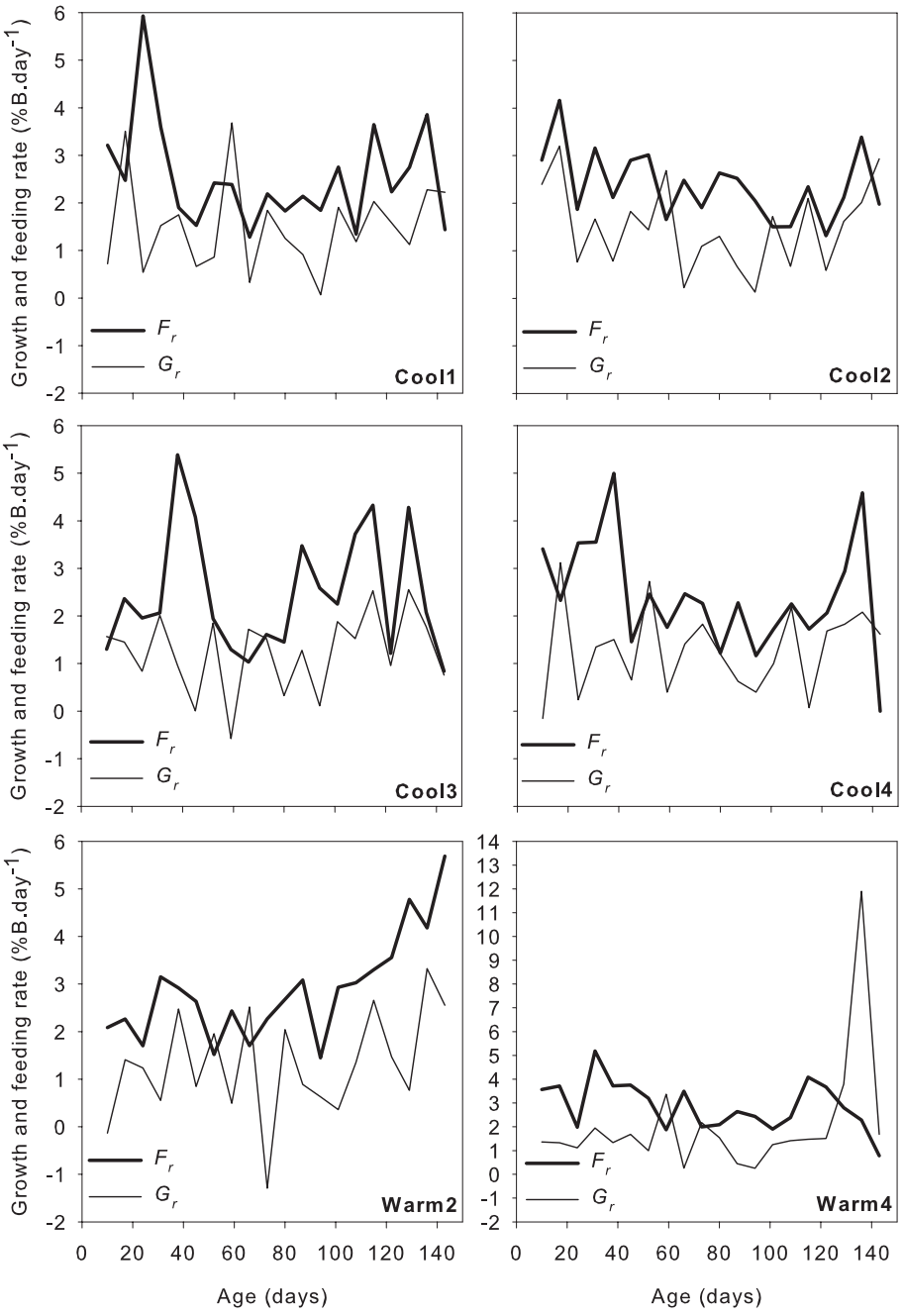

Fig. 2.3 Standardised feeding rate F_r and growth rate G_r (in % body weight per day) experienced by individual octopus. Note the change of scale for Warm4.

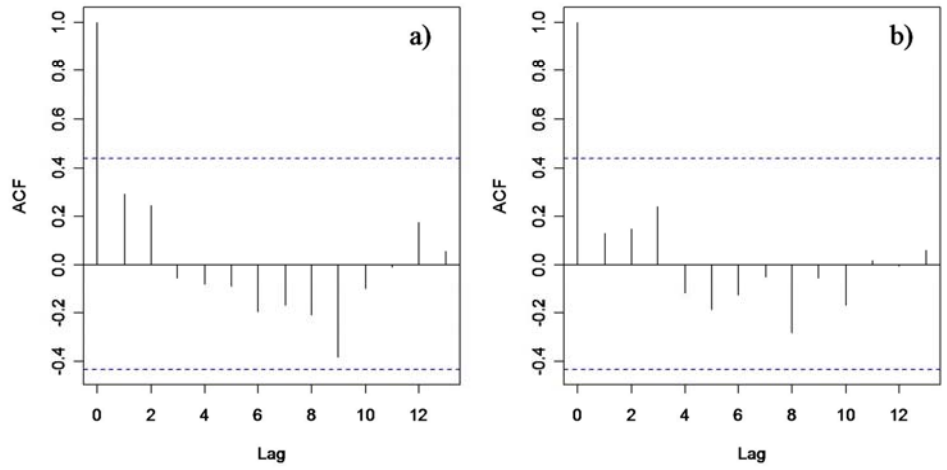

Fig. 2.4 Autocorrelation plots of the average feeding rate F_r (in % body weight per day) under a) the cool temperature regime (n = 4), and b) the warm temperature regime (n = 2). Bars that protrude beyond the dotted lines indicate significant correlations.

Food conversion rates C_r were variable from one week to the next (Fig. 2.5), ranging from -8.10 to 70.40%.d^{-1} under the warm regime (mean % per day ± SE = 9.57 ± 1.93, n = 40) and from -6.30 to 23.90%.d^{-1} for octopus reared under the cool treatment (mean = 8.61 ± 0.67, n = 79). C_r could not be calculated for Cool4 between day 136 and 143 since this individual consumed no food during this period. Food conversion rate is however expected to exceed 100%.d^{-1} for that period since substantial growth was observed despite the lack of food intake. Only individual Warm2 displayed evidence of periodicity in food conversion rate with a highly significant negative autocorrelation at lag 1 (Fig. 2.6a).

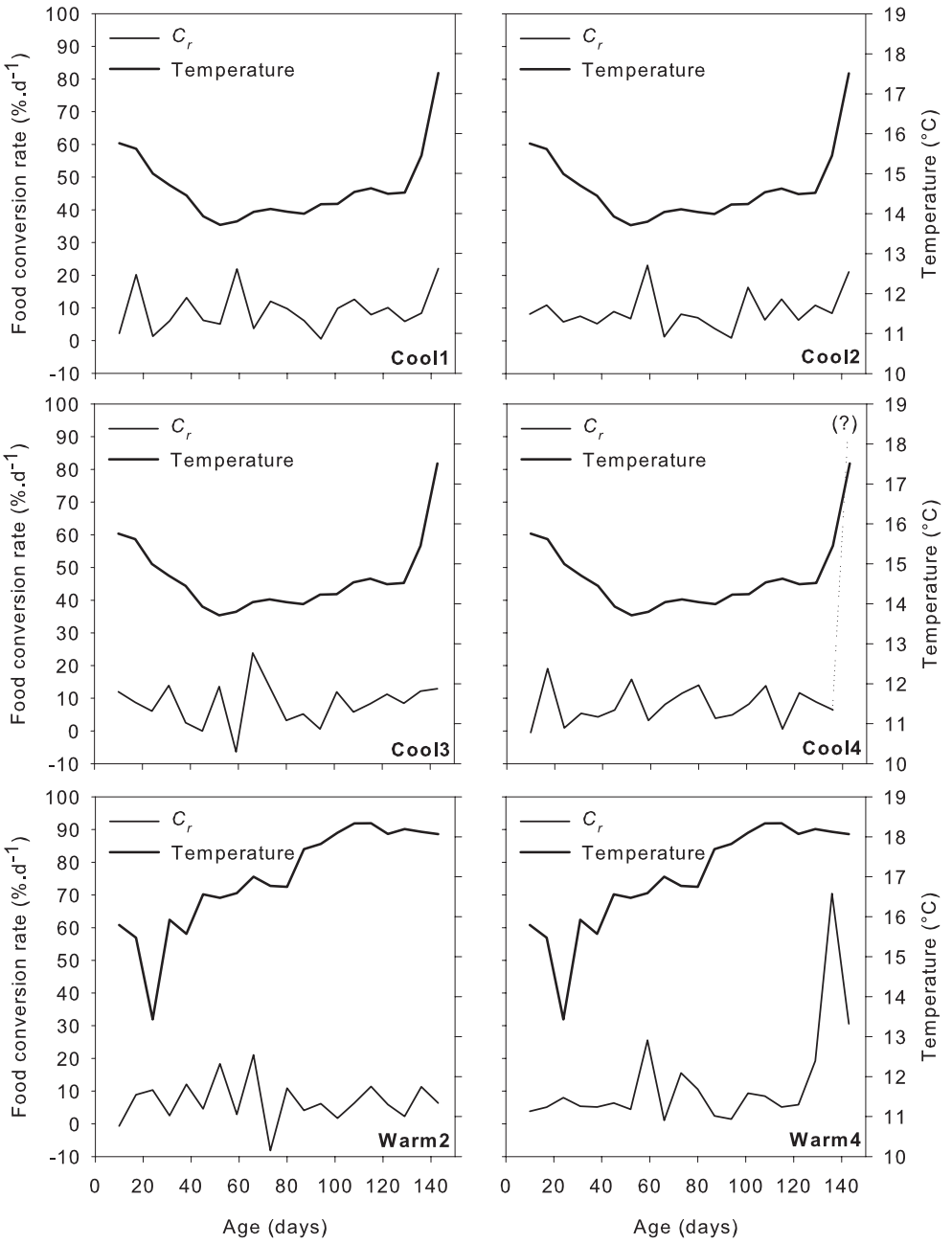

Fig. 2.5 Standardised food conversion rate C_r (in % per day) and temperature experienced by individual octopus. It was not possible to calculate C_r between day 136 and day 143 for Cool4.

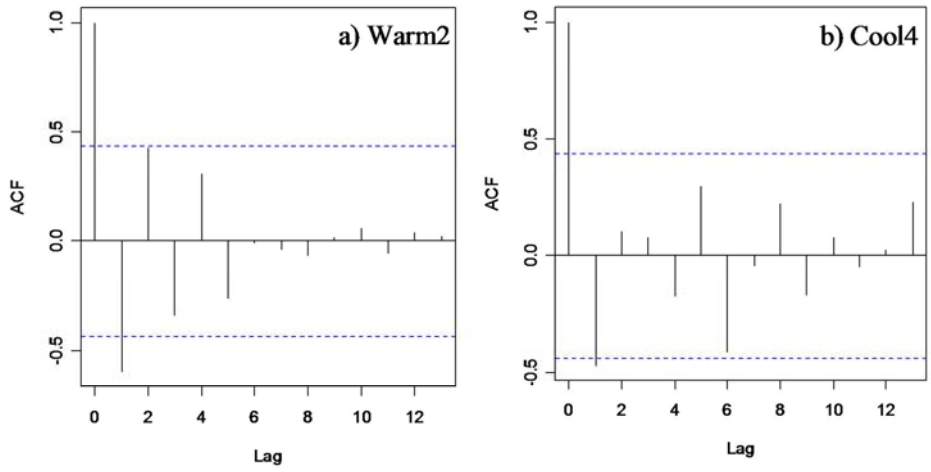

Fig. 2.6 a) Autocorrelation plot of food conversion rate for Warm2; b) autocorrelation plot of growth rate for Cool4. Bars that protrude beyond the dotted lines indicate significant correlations.

Individual growth under both temperature regimes was best described by an exponential curve (Fig. 2.7) with adjusted r^2 values for individual growth trajectories ranging between 0.91 and 0.99. The mean best fit growth curve was $B = 0.227e^{0.015t}$ under the warm regime and $B = 0.264e^{0.013t}$ under the cool regime. Octopus under the warm regime (growth rate $m = 0.015$) grew faster than those under the cool regime ($m = 0.013$). Warm4 exhibited a two-phase growth pattern in which a striking change in body weight occurred at around 133 days (Fig. 2.7). The resulting two-phase growth curve is best described by the exponential equations: $B = 0.208e^{0.014t}$ ($r^2 = 0.987$) from 0 to 133 days and $B = 0.3142e^{0.017t}$ ($r^2 = 1$) from 133 to 143 days.

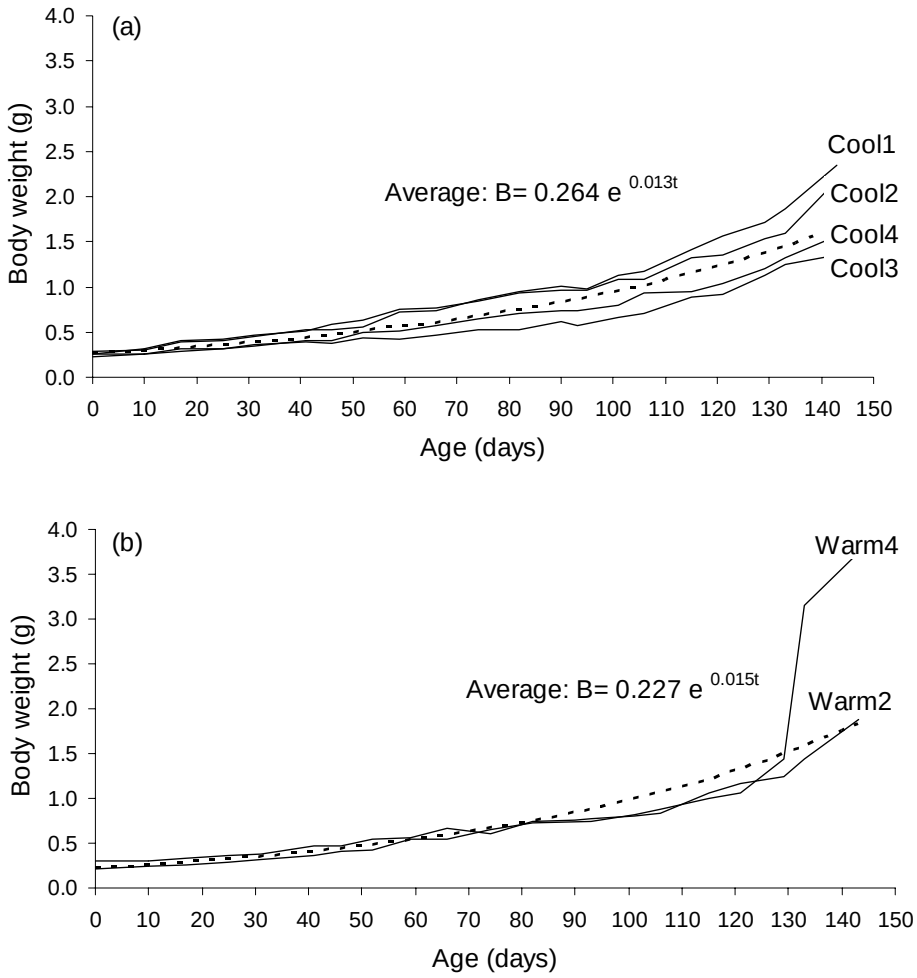

Fig. 2.7 Raw data of individual (—) and average (---) growth under the a) cool and b) warm temperature regime.

In close agreement with the exponential growth rate coefficients *m* obtained from the regression models described above, the mean growth rate G_r (% body weight per day ± SE) was 1.67± 0.31 under the warm regime (range = -1.29 − 11.89% body weight.day^{-1}, n = 40) compared to 1.38± 0.10 under the cool regime (range = -0.57 − 3.68% body weight.day^{-1}, n = 80). Although there appeared to be some regular fluctuations in the growth rate time series of all individuals (Fig. 2.3), only Cool4 displayed a

statistically significant periodicity in G_r, with a negative cross-correlation at lag 1 (Fig. 2.6b).

Effect of temperature on F_r, G_r and C_r

Overall, cross-correlation analyses suggested that changes in temperature did not drive changes in F_r, or G_r or C_r. Analysis of the mean C_r time series for the cool regime showed a significant positive cross-correlation between T and C_r at lag 0 (r = 0.64) (Fig. 2.8a), suggesting that changes in food conversion rates in the current week were correlated with changes in temperature. This significant correlation was most likely influenced by individual Cool4, which displayed a similar cross-correlation pattern with temperature (r = 0.68 for lag 0) (Fig. 2.8b). The absence of significant cross-correlations for the other five individuals suggests that temperature had a minimal effect on C_r. No significant cross-correlations were obtained between the mean F_r time series and temperature, or between individual F_r time series and temperature (Fig. 2.8c and 2.8d), suggesting that changes in temperature had no effect on feeding rate. Similarly, temperature appeared to have no influence on growth rate as revealed by the absence of significant cross-correlations between mean G_r time series, or individual G_r time series, and temperature (Fig. 2.8e and 2.8f).

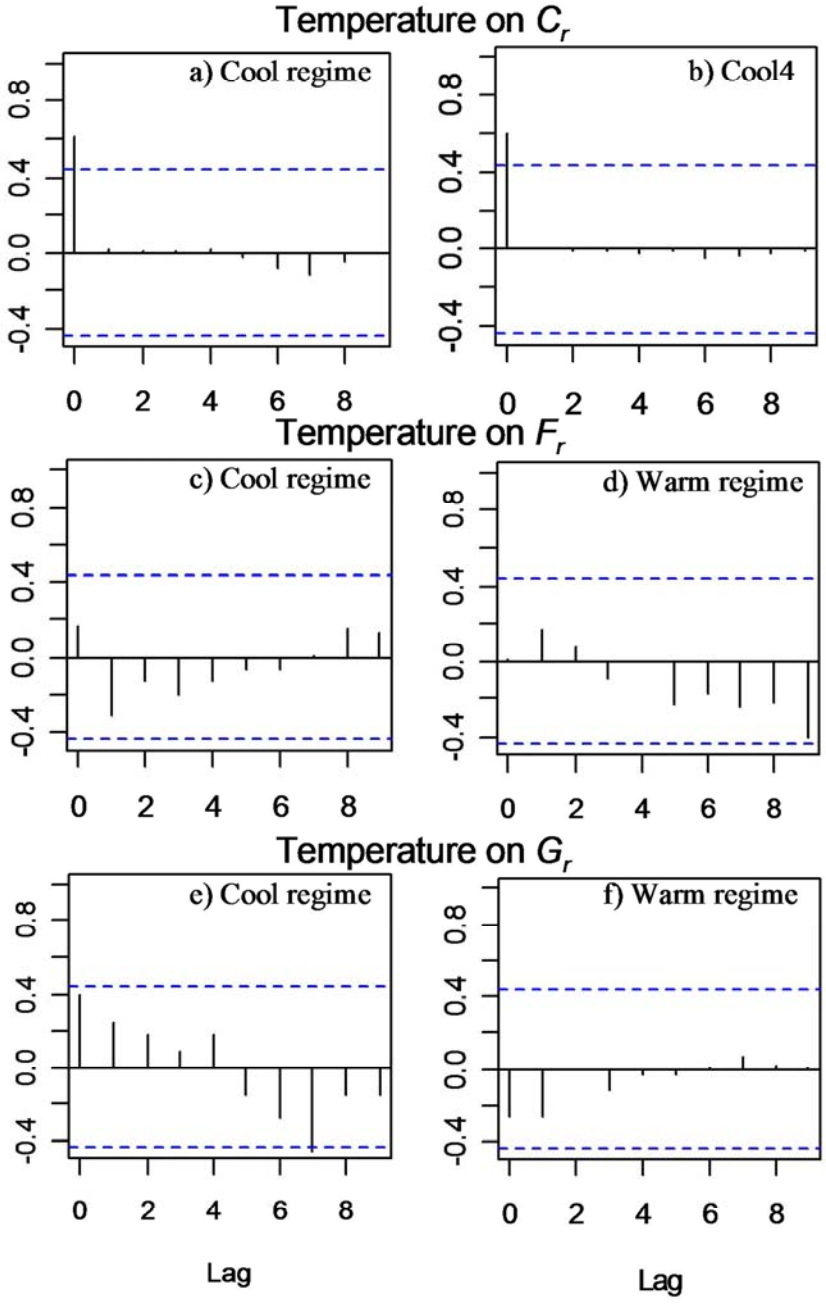

Fig. 2.8 Cross- correlation plots showing the influence of temperature T on feeding rate F_r, growth rate G_r and food conversion rate C_r: a) T on the mean C_r for the cool regime; b) T on C_r for individual Cool4; c) T on the mean F_r for the cool regime; d) T on the mean F_r for the warm regime; e) T on the mean G_r for the cool regime; f) T on the mean G_r for the warm regime. Bars that protrude beyond the dotted lines indicate significant correlations.

Feeding rate and growth rate

Interestingly, fluctuations in feeding rate did not appear to drive fluctuations in growth rate as evidenced by the absence of significant cross-correlations of F_r on G_r (Fig. 2.9a and 2.9b). Fluctuations in G_r however influenced fluctuations in F_r under the warm regime, with a positive cross-correlation of G_r on F_r at lag 1 (Fig. 2.9c). This significant correlation was most likely influenced by individual warm2, which displayed a similar cross-correlation pattern (Fig. 2.9d). The absence of significant cross-correlations for the other five individuals suggests that the effect of G_r on F_r is minimal.

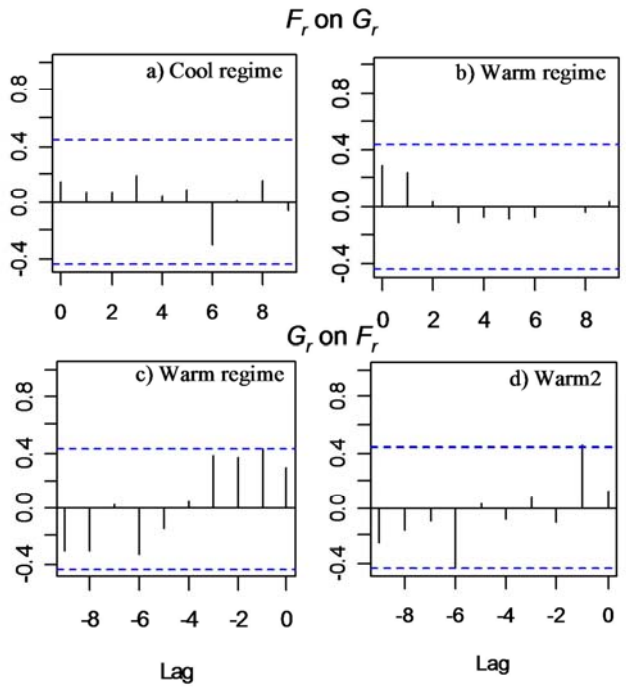

Fig. 2.9 Cross-correlation plots showing the relationship between feeding rate F_r and growth rate G_r: a) mean F_r on mean G_r for the cool regime; b) mean F_r on mean G_r for the warm regime; c) mean G_r on mean F_r for the warm regime; d) G_r on F_r for Warm2. Bars that protrude beyond the dotted lines indicate significant correlations.

Feeding rate and food conversion rate

Analysis of the mean time series showed a significant negative cross-correlation at lag 0 for C_r on F_r under the cool regime (r = -0.68) (Fig. 2.10a). This significant relationship was mainly due to consistent negative cross-correlations exhibited by all individuals for C_r on F_r at lag 0, even though only that of Cool4 was statistically significant at this lag (r = -0.63) (Fig. 2.10c). The analysis for individual Warm4 also revealed a significant negative cross-correlation at lag 0 (r = -0.79) (Fig. 2.10e), although no such pattern was evident from the analysis of the mean time series for the warm regime (Fig. 2.10d). Overall, individuals that demonstrated a high food conversion rate tended to have a low feeding rate in the same week, and vice versa. Fluctuations in food conversion rate also appeared to drive fluctuations in feeding rate in subsequent weeks for some individuals. Analysis of the mean time series of C_r on F_r for the warm regime revealed a significant positive cross-correlation at lag 3 (Fig. 2.10d). This was mainly due to positive cross-correlations at this lag exhibited by Warm2 and Warm4, even though none of them was statistically significant. Analysis of the mean time series of C_r on F_r for the cool regime did not reveal any significant cross-correlations although the analysis for individual Cool3 revealed a significant positive cross-correlation at lag 4 (Fig. 2.10b).

Interestingly however, the cross-correlation analysis of F_r on C_r revealed that there were no significant correlations for any individual, which suggests that fluctuations in C_r were not determined by fluctuations in F_r.

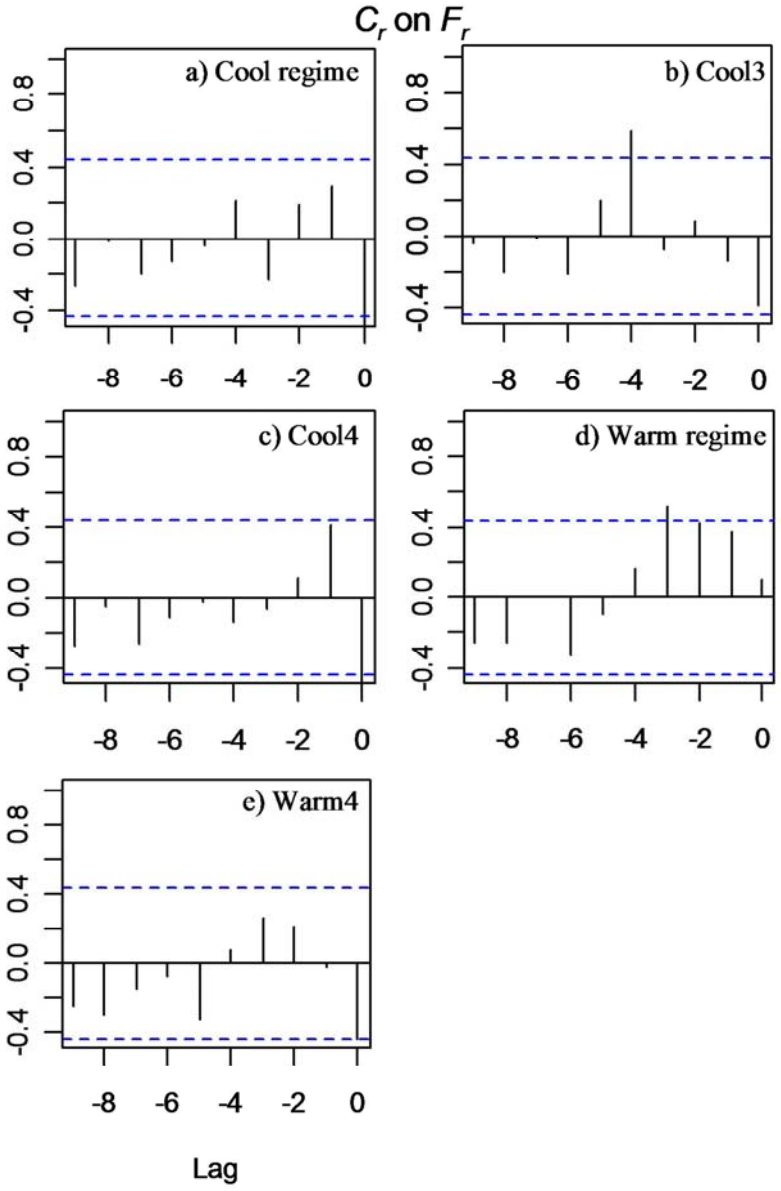

Fig. 2.10 Cross-correlation plots showing the relationship between food conversion rate C_r and feeding rate F_r: a) mean C_r on mean F_r for the cool regime; b) C_r on F_r for Cool3; c) C_r on F_r for Cool4; d) mean C_r on mean F_r for the warm regime; e) C_r on F_r for Warm4. Bars that protrude beyond the dotted lines indicate significant correlations.

Growth rate and food conversion rate

The time series for G_r and C_r supported the existence of a relationship between G_r on C_r with evidence of a positive cross-correlation occurring at a time lag of under a week (lag 0). All individuals but Cool4 had statistically significant cross-correlations at lag 0 ($0.85 < r < 0.97$) (Fig. 2.11). The lack of a significant correlation for this individual can be accounted for by the fact that Cool4 exhibited an extremely high C_r ($238\%.d^{-1}$) and was hence an outlier. Individual cross-correlation plots of G_r on C_r and C_r on G_r did not show any other significant correlations, suggesting that changes in one variable did not affect the other variable in time.

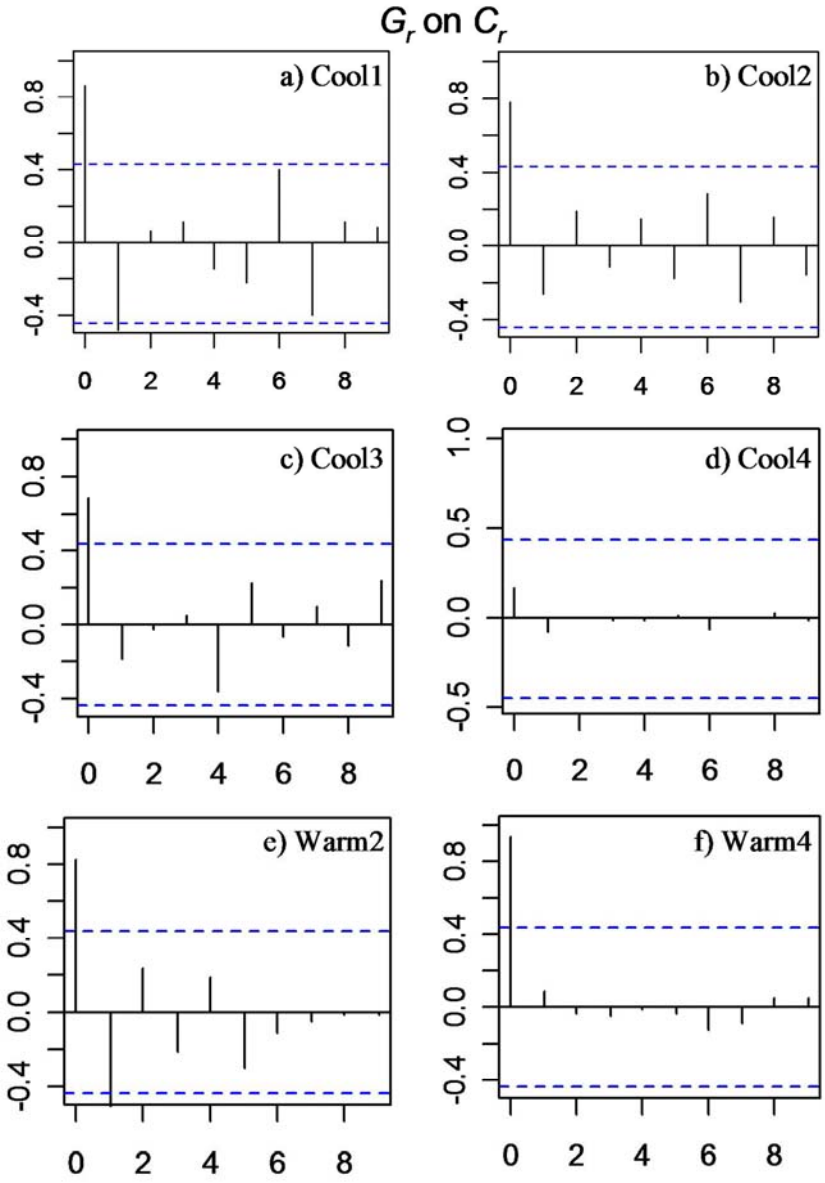

Fig. 2.11 Cross-correlation plots of food conversion rate C_r on growth rate G_r for: a) Cool1; b) Cool2; c) Cool3; d) Cool4; e) Warm2; f) Warm2. Bars that protrude beyond the dotted lines indicate significant correlations.

DISCUSSION

The relationship between F_r, G_r, C_r and T is highly complex with this detailed study revealing unexpected results such as the lack of a correlation between feeding rate and growth rate, and the observation that dynamic temperatures have little effect on any of the variables examined. Strong individual variability was evident and may in part be explained by the dynamic growth process.

Food consumption, food conversion rate and growth rate

As for other octopuses reared in laboratory conditions (Nixon 1966; Mather 1980; Boyle and Knobloch 1982; Houlihan et al. 1998), individuals did not feed everyday potentially as a consequence of stress in captivity (Houlihan et al. 1998). Feeding rates were comparable to those of sub-adult or adult octopus from other species (Boyle and Knobloch 1982; Mangold 1983a; Houlihan et al. 1998; Segawa and Nomoto 2002) but were much lower (0.10 to 5.93%.d^{-1}) than feeding rates of 18.8 to 32.3%.d^{-1} found for captive juvenile *Octopus ocellatus* (Segawa and Nomoto 2002). Mean food conversion rates found for *O. pallidus* were higher than that reported for immature *Octopus tehuelchus* (Klaich et al. 2006) another species with benthic hatchlings (4.4%.d^{-1} at 15°C and 5.2%.d^{-1} at 10°C- calculated from the original food conversion in %). Food conversion rates were highly variable on a weekly basis, with C_r as high as 70.4%.d^{-1}. Similar weekly

fluctuations have been reported in previous studies (Mangold and von Boletzky 1973; Mangold 1983a; Mangold 1983c). One individual displayed a C_r in excess of 100%.d^{-1} which suggests that all the growth observed can not be explained by current or very recent food intake.

Growth trajectories were exponential throughout the experimental period but animals did not display two-phased growth (exponential growth phase followed by a slower growth phase) as observed for other cultured octopus species (Forsythe and Van Heukelem 1987; Semmens et al. 2004). Growth rates of 1.38% and 1.67% for the cool and warm treatment respectively were comparable to the values of 1.43% (cool treatment) and 1.73% (warm treatment) found by Leporati et al. (2007) for *O. pallidus* hatchlings reared under fluctuating temperature regimes similar to those employed in this study.

Food consumption, food conversion and growth rates all exhibited fluctuations over time. These fluctuations showed no statistically significant periodicity on a weekly basis but may be linked to some underlying physiological growth mechanism, as discussed further below (p 47).

Effect of temperature on F_r, G_r and C_r

Temperature is one of the most important abiotic factors affecting the physiology of poikilothermic animals. The lack of relationship between food conversion rate and temperature in the present study is consistent with results of previous studies on cephalopods (Mangold and von

Boletzky 1973; Mangold 1983a) which found that food conversion rate had no dependence on temperature. Temperature-dependence of growth rate and feeding rate is, on the other hand, well established for octopus, with higher temperatures resulting in higher food intake (Mangold and von Boletzky 1973; Joll 1977; Segawa and Nomoto 2002) and growth (Semmens et al. 2004) within the thermal range of a species. The lack of statistical support for a relationship between F_r and temperature or G_r and temperature in this study may be connected with a complex response to the fluctuating temperature regime. Since maintenance costs are temperature-related (Wells and Clarke 1996), short-term fluctuating temperatures would most likely produce variations in maintenance costs that must ultimately result in variations in growth. This could obscure a direct dependence of growth on temperature. The substantial variations observed in food conversion rates could also have contributed to the lack of a strong relationship between growth and temperature as suggested by Joll (1977). The pattern observed in this study is however more likely to reflect the situation in the wild since short-term environmental temperature fluctuations would be frequently encountered by octopus, either from individuals moving between deep and shallow waters or through exposure to different water masses.

Relationship between F_r, G_r and C_r

Fluctuations in feeding rate did not appear to drive fluctuations in growth rate, which suggests that the energy from food may not be utilised for

immediate weight gain. There appeared to be no feedback between growth and feeding as growth rates in a given week did not influence feeding rates in subsequent weeks and vice versa.

Fluctuations in feeding rate did not appear to affect food conversion rate, suggesting that energy from food was not translated into an increase in weight on a regular basis. Interestingly however, food conversion rate appeared to have an immediate impact on feeding rate. The negative cross-correlations between these two variables suggest that the physiological mechanism underlying food conversion may have an immediate antagonist effect on feeding. The observation that current food conversion rates could have an impact on feeding rates 3 weeks later in some individuals illustrates the length of time lag which may be involved.

The results obtained in this study may in part be explained by the dynamic growth process. Cephalopods grow through hyperplasia (i.e. generation of new muscle fibres) and hypertrophy (i.e. the increase in size of existing muscle fibres) throughout their lives (Pecl and Moltschaniwskyj 1997; Moltschaniwskyj 2004). These two processes are likely to be different in terms of energy demand and weight gain produced: hyperplasia is likely to be energetically costly (due to the creation of new fibres and structural elements) with potentially little weight gain, whereas hypertrophy may be less energy-demanding (expansion of muscle fibres can be achieved by increasing intracellular

fluid level) but produce larger weight gains. If growth consists of an alteration between phases of predominantly hyperplasic growth followed by phases of predominantly hypertrophic growth, growth rate (and food conversion rate) would also fluctuate accordingly with phases of low G_r corresponding to hyperplasia and phases of high G_r corresponding to hypertrophy. This could explain why biochemical techniques used to estimate instantaneous growth rate have had mixed success in octopus and cephalopods in general (Semmens and Jackson 2005). High RNA concentrations, which in octopus show a linear relationship with rates of protein synthesis (Houlihan et al. 1990), may not reflect a period of high growth rate if the individual is undergoing hyperplasia. Such a growth mechanism could also result in C_r values in excess of 100% as observed in this study if the amount of food consumed is small in relation to the weight gained through hypertrophy of the muscle cells.

The relative length of the hypertrophic/hyperplasic phases is speculative at this stage but the lack of periodicity in feeding rates, growth rates or conversion rates suggest that these phases may not be physiologically fixed and could be influenced by external factors.

The validity of this hypothesis needs to be formally tested through further experimental work. Precise measurements of F_r, G_r, C_r and T in aquaria along with histological analysis of muscle tissue from various parts of the mantle would be required to identify whether an alternation between hyperplasia and hypertrophy does occur. Also, the time scale of one week

for the measurement of variables may not be adequate to capture all the processes in place and choosing shorter time-scales may reveal additional information.

CONCLUSION

The relationship between food consumption, food conversion rate, growth and temperature during the early life-history of octopus is complex. Temperature unexpectedly did not appear to produce a statistically significant impact on feeding, growth or food conversion rates. Feeding rate also did not appear to impact food conversion rate or growth rate. Short periods of starvation were common and the high values obtained for food conversion rate for some individuals suggest that octopus can grow substantially with little or no food intake, which possibly implies that a re-evaluation of our understanding of the way octopus growth occurs is necessary. Individual variability observed in octopus growth may be dependent on the growth mechanism involved, more specifically the fine balance between the hyperplasic and hypertrophic growth found in cephalopods. This study highlights the extreme plasticity and complexity of cephalopod growth and the need for further work in this area.

Ch 3

Modeling the impact of temperature on the growth pattern of octopus using bioenergetics

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ABSTRACT

In octopus, growth trajectories have implications for survivorship, adult size and fecundity. Based on the concept that growth is bi-phasic and that energy conservation enforces the shift between the two growth phases, a temperature-dependent model is developed, which incorporates the energy balance between food intake and expenditure in growth and metabolism. The model is employed to investigate growth patterns occurring at different temperatures for two octopus species, *Octopus ocellatus* and *Octopus pallidus.* Model projections were consistent with laboratory data and suggest that increases in temperature as small as 1°C could have a significant influence on cephalopod growth, affecting the threshold body mass by up to 15.5% and the body mass at 100 days by up to 62.6%. Sensitivity analyses suggest that threshold size is more sensitive than threshold age to any given change in parameter values, and that metabolic rate has the greatest influence on the growth threshold. This model provides a basis for predicting individual growth trajectories and consequential the population structure of natural octopus populations.

INTRODUCTION

One of the most remarkable characteristics of octopus is their energy efficiency, which allows them to sustain high growth rates during their short lifespans (usually < 18 months) while maturing and reproducing. This is facilitated by a generalist diet, very high consumption rates, high conversion rates, efficient use of oxygen and their unique ability, like most cephalopods, to sustain continuous hyperplastic and hypertrophic muscle growth (Jackson and O'Dor 2001; Semmens et al. 2004). However, despite recent advances in this area (Wells and Clarke 1996; Daly and Peck 2000; Petza et al. 2006), our understanding of the energetics of octopus growth remains sketchy and there are still debates as to the actual form of the growth curve for wild animals. Analyses of field data may never shed light on this issue as field size-at-age data for species such as squid typically contain few data for the early part of the life span and frequently exhibit a greater scattering of data points with increasing age (Arkhipkin and Roa-Ureta 2005). This induces serious difficulties into statistical approaches which depend only on regression inference to estimate the individual growth curve, so that the curve may often be mis-specified when data are inadequate to support the relationship being fitted.

Grist and Jackson (2004) introduced the concept of energy balance as a mechanism which might lead to two-phase growth in cephalopods. After reaching a critical size, the authors hypothesised that the energy intake from food would no longer sustain the energetic demands of metabolism

and individual growth at the current level. As a consequence, individuals are predicted to shift to a slower growth rate, thus resulting in a two-phase growth pattern. While taking account of body size, this model does not explicitly invoke environmental temperature, which is the most important abiotic factor influencing cephalopod life history alongside nutrition. Since temperature influences all aspects of the energy budget, and, according to the hypothesis of Grist and Jackson (2004), energetics determine the transition between the two growth phases, temperature must therefore influence the transition body mass and transition age out of exponential growth, and consequently individual growth trajectories. This has implications for survivorship (Calow 1987), adult size (Forsythe and Van Heukelem 1987) and hence fecundity (Mangold 1987) at the individual level, subsequently influencing population structure. Assessing the effect of temperature on the growth of octopus is therefore crucial to understanding the population dynamics of these short-lived and increasingly exploited species, particularly in the light of predicted warming of the oceans. The aims of this chapter are

(1) to develop a temperature-dependent energy balance model describing growth in octopus, and (2) to investigate the influence of temperature on the energetics of octopus, and its associated impact on growth patterns.

THE ENERGY BALANCE MODEL

Concept

The traditional formulation of the energy budget of marine animals is based on the balanced energy equation formulated by Winberg (1956), which follows the fundamental law of energy conservation

$$F_T = M + G + W \tag{5}$$

where F_T is the total energy intake rate from food, M and G are the respective rates at which energy is expended in metabolism and growth (both somatic and reproductive), and W is the rate at which energy is wasted in excretions such as urine, faeces and other wastage (e.g. mucus, shed sucker cuticles). These rates are expressed in kj per day (kj. day^{-1}). Unlike somatic growth, reproductive growth in octopus differs between sexes in both energy allocation and timing. Males appear to mature earlier, coinciding with the shift between growth phases, whereas females tend to mature in the second slower phase of growth (Semmens et al. 2004). Assessing reproductive investment has been achieved for a few species (Boyle and Knobloch 1984; Perez and Haimovici 1991; Cortez et al. 1995) but estimating the onset of sexual maturation remains problematic, as the influence of food availability and temperature on this aspect of reproduction has yet to be quantified. Given the deficiency in information, reproductive growth was not incorporated in the model to avoid

introducing unsupportable complexity. The current representation is consequently characteristic of females' energetics.

The rate W (waste) can be expressed by way of an assimilation efficiency parameter A_e, defined as the proportion of the intake energy which is not lost in excreta (Kleiber 1947), so that

$$F_T \times A_e = F = M + G \tag{6}$$

In order for an individual to survive there must be sufficient energy available to support metabolism and growth so that $F \geq M + G$ or equivalently $F - M - G \geq 0$, which hence gives rise to an energy balance constraint (Grist and Jackson 2004).

The dependencies of metabolic rate M and food intake rate F on body mass B have previously been characterised by an allometric scaling law of the form $Y = qB^p$ where $p > 0$ is a scaling exponent, $q > 0$ is a constant, and Y is M or F (West et al. 1997; Boyle and Rodhouse 2005; O'Dor et al. 2005) . The growth rate G during the exponential phase is (by definition) directly proportional to body mass. Hence, the required supply of energy $E(B)$ can be expressed as a function of body mass B

$$\begin{aligned} E(B) &= F(B) - M(B) - G(B) \\ &= q_1 B^{p_1} - q_2 B^{p_2} - q_3 B \end{aligned} \tag{7}$$

where $E(B)$ must remain positive in order for an individual to survive (Fig. 3.1).

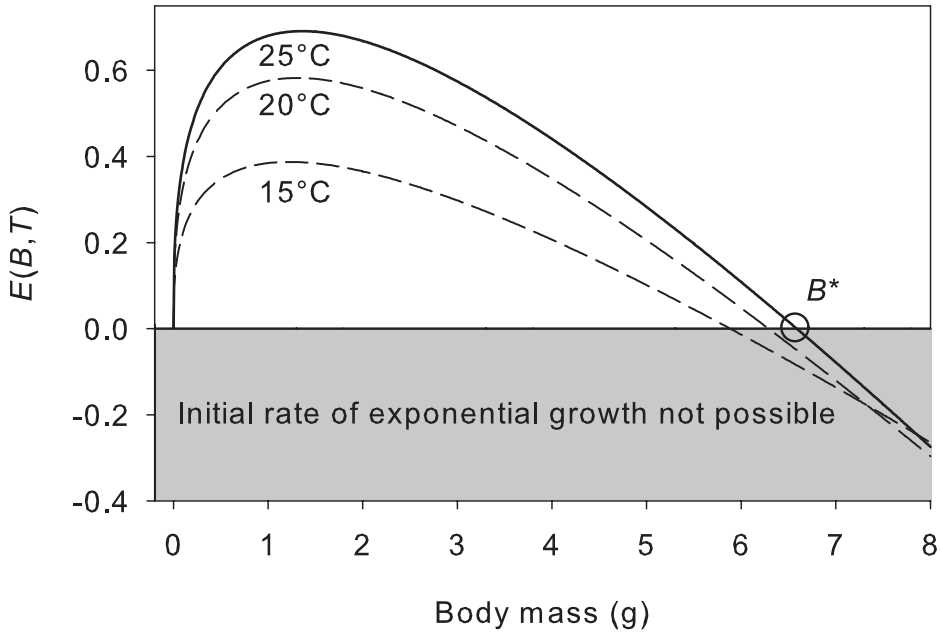

Fig. 3.1 Plot of the energy balance function $E(B,T)$ when parameterised for individuals reared at 15°C, 20°C and 25°C with data obtained from Experiment 1. By definition, threshold body mass B^* is reached when $E(B,T) = 0$. Where A is the size at hatching and m is a growth rate coefficient, beyond a critical body weight B^* achieved at age t^* (where $B^* = Ae^{mt^*}$), it follows that an individual would be unable to support its total energy expenditure. Grist and Jackson (2004) hypothesised that a shift from exponential growth would then be necessary.

The value of 0.75 has been traditionally assigned as the scaling exponent of metabolism p_2 for many animals (Kleiber 1932), however, octopus generally have higher p_2 values which may reach up to 0.90 (Katsanevakis et al. 2005). The q_i are generally species' specific (West et al. 1997) and are typically estimated from experimental studies.

Incorporation of temperature dependency: the temperature-dependent energy balance model (TEBM)

Since temperature T affects feeding, metabolic and growth rates in cephalopods, temperature dependency is incorporated by modifying $E(B)$ to $E(B,T)$ and through specifying q_i as temperature dependent $q_i(T)$ so that

$$\begin{aligned} E(B,T) &= F(B,T) - M(B,T) - G(B,T) \\ &= q_1(T)B^{p_1} - q_2(T)B^{p_2} - q_3(T)B \end{aligned} \tag{8}$$

where the functions $q_i(T)$ were empirically determined from temperature dependent data sets. All body mass exponents p_i were assumed to be species specific and independent of temperature as noted with p_2 by Zeuthen (1953), von Bertalanffy (1957) and Katsanevakis et al. (2005).

METHODS

We parameterised the model for both *O. ocellatus* and *O. pallidus*. Model parameters for each species were estimated from data published in the literature and collected in laboratory experiments, henceforth referred to as Experiments 1, 2 and 3. Parameter values for both species are summarised in Table 3.1.

Table 3.1 Parameter values for the temperature-dependent energy balance model. B is the body weight of the octopus (g), T the temperature (°C), (pal) indicates references for *O. pallidus* and (oc) references for *O. ocellatus*.

Eq. no	Parameters		*O. pallidus*	*O. ocellatus*	Source
(13)	**Growth rate:** $q_3(T)B = k_3\left(m_{opt} - d\left(T_{opt} - T\right)^2\right)B$				
	Optimum temperature for growth (T_{opt}) (°C)		16.5	25	(1)pal, (2)oc
	Growth rate at T_{opt} (m_{opt}) (g.day^{-1})		0.0167	0.0750	(1)
	Parabolic constant (d)	if $T \leq T_{opt}$	0.00039	0.00026	(1)
		$T > T_{opt}$	0.00039	0.0015	(1)
	Energy equivalent of octopus tissue (k_3) (kj.g^{-1})		4.05848	4.05848	(3)
(15)	**Feeding rate:** $q_2(T)B^{p_1} = \left(f_{opt} - d_f\left(T_{fopt} - T\right)^2\right)B^{p_1}$				
	Assimilation efficiency (A_e)		90%	90%	(4)
	Energy equivalent of food (k_f) (kj.g dw^{-1})		6.82353	11.05	(5)pal, (6)oc
	Conversion coefficient wet to dry weight ($k_{w/d}$)		0.249	0.339	(1)pal, (6)oc
	Optimum temperature for feeding (T_{fopt}) (°C)		18.4	28.6	(1)
	Feeding rate at T_{fopt} (f_{opt}) (kj.day^{-1})		0.584	1.064	(1)
	Parabolic constant (d_f)	if $T \leq T_{fopt}$	0.0083	0.0025	(1)
		$T > T_{fopt}$	0.0276	0.0920	(1)
	Feeding rate exponent (p_1)		1.17	0.39	(1)
(16)	**Metabolic rate:** $q_2(T)B^{p_2} = k_1 e^{\left(a_2 + \frac{b_2}{T + k_2}\right)} B^{p_2}$				
	Metabolic rate exponent (p_2)		0.88	0.81	(1)pal, (2)oc
	Conversion factor O_2 mg.h^{-1} to kj. day^{-1} (k_1)		0.33758	0.33758	(7) and (8)
	Conversion factor °K to °C (k_2)		273.15	273.15	
	Constant (a_2)		21.80	21.80	(9)
	Constant (b_2)		-6952.8	-6952.8	(9)

Source: (1) Present study, (2) Segawa and Nomoto (2002), (3) O'Dor and Wells (1987), (4) Wells et al. (1983), (5) Perez et al. (2006), (6) McKinney et al. (2004), (7) Prosser (1973), (8) Elliot and Davison (1975), (9) Katsanevakis et al. (2005).

Data sets

Experiment 1 provided data on the growth and feeding rates and oxygen consumption of *O. ocellatus*, details of which are published in Segawa & Nomoto (2002). Eleven juveniles hatched in captivity were reared for 205 days at 20±1C^{o} (n = 6) and 25±1C^{o} (n = 5). Individuals were fed hermit crabs *Clibanarius virescens* and *Pagurus spp*. ad libitum. Individual food consumption was measured daily and octopus were weighed every 6–14 days to assess growth. The oxygen consumption curves provided the species specific metabolic exponent p_2, which was calculated as the mean p_2 value obtained under the two temperature treatments. One individual in the 20^{o}C treatment died at 63 days of age and was excluded from the present analyses because there were too few datapoints to establish valid feeding and growth curves.

Experiment 2 provided data on the growth rates and feeding rates of *O. pallidus*, details of which are presented in Chapter 2. For the purpose of this chapter, temperature in each treatment was averaged over the duration of the experiment, so that juveniles were reared for 143 days at 14.7±0.08^{o}C SE (n = 4) and 16.9±0.12^{o}C (n = 4). While two individuals died in the 16.9C^{o} treatment before the end of the experiment, only that which died at 57 days of age was excluded from the analyses as there were too few datapoints to establish valid feeding and growth curves for the purpose of this study.

Experiment 3 provided data on the metabolism of *O. pallidus*. The purpose of the experiment was to estimate the species metabolic rate exponent p_2 (eq. 7). Details of the experimental procedure are provided below.

Experimental estimation of p_2 for *O. pallidus*

Hatchlings were reared from eggs in 250 l stock tanks under fluorescent lighting replicating natural daylight (06.00−18.00 hrs light, 18.00−06.00 hrs dark), and the oxygen consumption of two juvenile octopus were measured on three occasions at 94, 134 and 148 days of age. All measurements were taken between 10am and 3 pm while the animals were in post-digestive conditions (at least 12 hours after feeding). Animals were placed in individual 600ml clear plastic respirometers and a gentle flow of oxygenated water was passed through the respirometers for a period of 1 hour in order to acclimatise the octopuses before measurements were taken (Fig. 3.2a). Care was taken to ensure that no air bubbles were trapped in the chambers. The water used in the respirometers was the same as that from the rearing tanks and was filtered (10 micron) before entering the chambers (Fig. 3.2b).

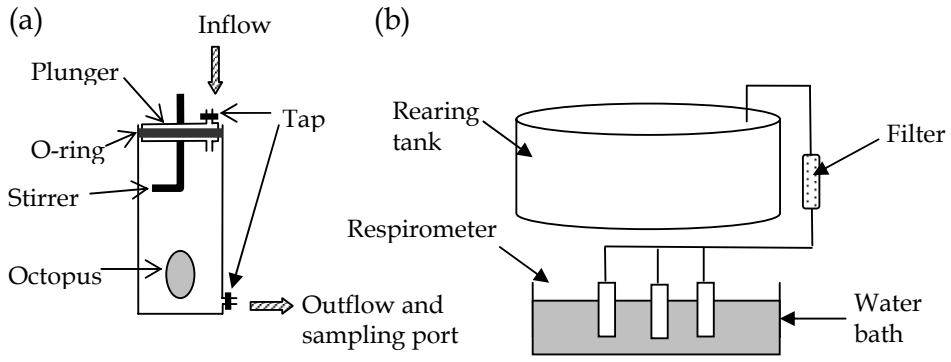

Fig. 3.2 a) Respirometer design and b) experimental setup for the oxygen consumption experiment.

Respirometers were immersed in a controlled temperature water bath to maintain a constant temperature of 18°C for the duration of the experiment. Three respirometers (#1-3) were set up for each temperature treatment (two with octopus and one blank). Octopuses were allocated randomly to respirometers to avoid any bias. After the acclimatisation period, respirometers were sealed by closing both taps. To ensure complete homogeneity of the sample, water was slowly mixed with a clear stirrer for 20 seconds before each sampling. This manipulation did not seem to disturb the octopus which did not display any colour changes, rapid movements or noticeable increase in ventilation.

Water was sampled through the outflow with a 20ml syringe ensuring that no air was drawn into the syringe. The outflow tap was opened and the respirometer plunger slowly pressed to expel water samples. The first 5 ml of water expelled was discarded as this corresponded to still water sitting in the outflow tube. The duration of the experiment was 180 min for the measurements at 94 days and 120 min for the measurements at 134

and 148 days. Water samples for oxygen analysis and temperature measurements were removed hourly. Oxygen concentration was determined using a modified Winkler titration method (Major et al. 1972, Crowley 1999). In the modified method, volume was scaled down to 20 ml and manganese sulphate solution and potassium iodide/sodium hydroxide solution were micropipetted directly into the syringe. Duplicate titrations were carried out for each sample (2x 10 ml titrations). All volumes of water extracted during the experiment were recorded precisely to correct the subsequent oxygen concentrations for volume. Oxygen consumption rate was calculated in µl O_2/g octopus/h and converted to kj.day^{-1} (see Table 3.1 for conversion rates). The best fit model, based on the highest r^2 value, was $M = 0.0546B^{0.8774}$ (Fig. 3.3), providing an estimated p_2 value of 0.88.

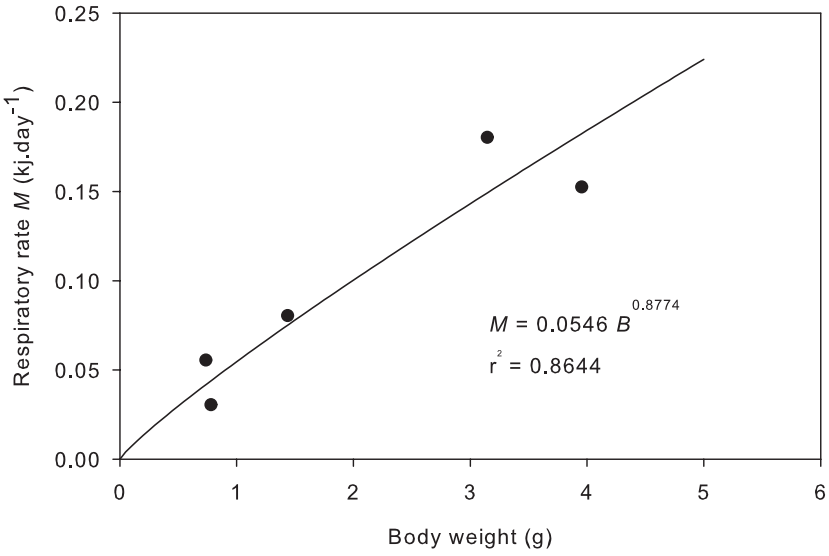

Fig. 3.3 Oxygen consumption *M* as a function of body weight *B* for juvenile *O. pallidus* at 18°C.

Experimental estimation of transition body mass and age

The method of Hatfield et al (2001) based on instantaneous relative growth rate (*IRGR*) was used to identify the transition point between the growth phases. If growth is exponential, the *IRGR* (i.e. the percent increase in body mass per day) will remain constant from measurement to measurement, although there will be some fluctuation as in any biological system (Hatfield et al. 2001). The point at which *IRGR* value starts to decline steadily marks the end of the initial exponential growth phase. The instantaneous growth rate for cephalopods following exponential growth is typically calculated according to the equation:

$$IRGR = \left(\frac{\ln B_2 - \ln B_1}{t_2 - t_1} \right) \times 100 \qquad (9)$$

where B_2 is the body mass at time t_2 and B_1 is the body mass at time t_1 (Forsythe and Van Heukelem 1987).

Using this method, we clearly identified a two-phase growth pattern for *O. ocellatus* individuals in Experiment 1 (Fig. 3.4) with a mean threshold age *t** in days ± 95% C.I. of 43 ± 27 days at 20C^{o} (range = 15–71 days, *n* = 5) and 37 ± 12 days at 25C^{o} (range = 25–49 days, *n* = 5), and a mean threshold body mass *B** in g ± 95% C.I. of 2.5 ± 3.5 g at 20C^{o} (range = 0–6.0 g, *n* = 5) and 2.3 ± 1.6 g at 25C^{o} (rang e= 0.7–3.9g, *n* = 5). No threshold was detected for *O. pallidus* in Experiment 2 as growth remained exponential during the duration of the experiment (Fig. 3.4).

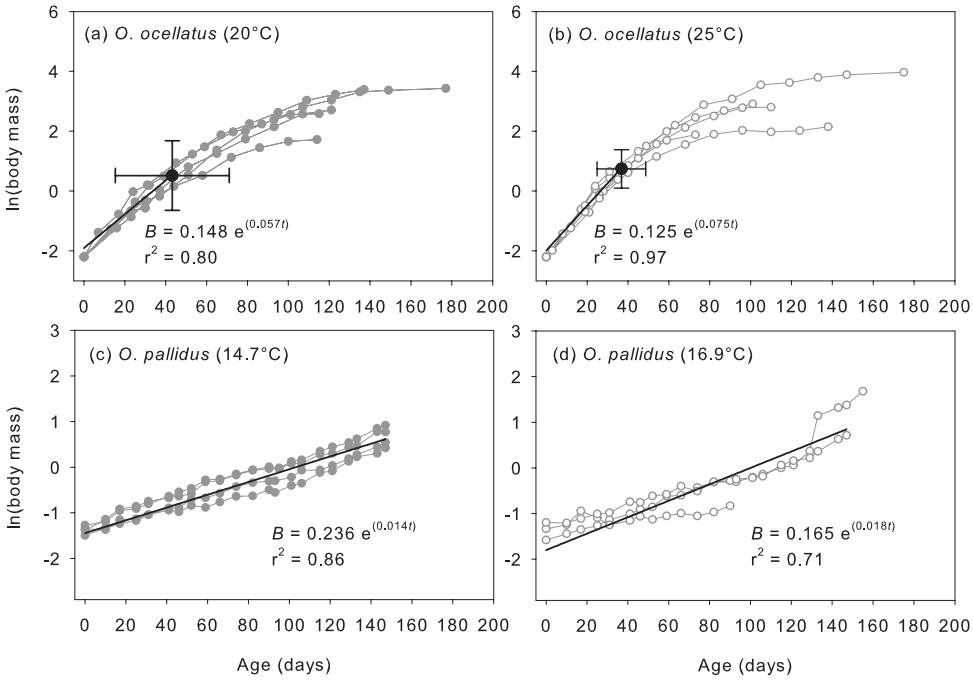

Fig. 3.4 Plots of individual growth curves for *O. ocellatus* at a) 20°C (n = 5) and b) 25°C (n = 5), and *O. pallidus* at c) 14.7°C (n = 4) and d) 16.9°C (n = 3). The solid black lines, estimated from nonlinear mixed-effect models, represent the mean growth curve for the initial growth phase and the black dots represent the mean transition age and body mass (± 95% confidence interval) out of the exponential growth phase.

Model parameterisation

Growth rate with $q_3(T) = k_3(m_{opt} - d(T_{opt} - T)^2)$

Growth studies have long established that temperature strongly influences the growth rate of cephalopods (e.g. Mangold and von Boletzky 1973; Forsythe and Hanlon 1988; Leporati et al. 2007). The dependency of growth rate on temperature in fish has been modeled with an inverted parabola to represent the general non-linear decrease in growth rate observed towards extreme temperatures (e.g. Ricker 1979; Bartsch 2002).

This model has a central optimum, corresponding to the maximum growth rate, and a symmetrical drop off on both sides. Based on this inverted parabolic function, the temperature mediation of growth rate coefficient m is given by

$$m(T) = m_{opt} - d(T_{opt} - T)^2 \tag{10}$$

where m_{opt} is the maximum value of $m(T)$ at the optimum temperature, d is a constant, T_{opt} is the optimum temperature for maximum growth and T is the ambient temperature. However, T_{opt} may not necessarily be the midpoint of the species' temperature range so that asymmetric curves might follow from introducing temperature limits on either side of the optimum (Bartsch 2002). The temperature-dependency of growth rate is then expressed by two equations

$$\begin{aligned} m(T) &= m_{opt} - d_1\left(T_{opt} - T\right)^2 \qquad T < T_{opt} \\ &= m_{opt} - d_2\left(T_{opt} - T\right)^2 \qquad T > T_{opt} \end{aligned} \tag{11}$$

During exponential growth at constant temperature, instantaneous growth rate (in g.day^{-1}) is given by

$$G(B) = \frac{dB}{dt} = mAe^{mt} = mB \tag{12}$$

where A is the hatchling size, m the growth rtae coefficient and B the body masss. This can be expressed in terms of its energy equivalent (in kj.day^{-1}) as a function of body mass with temperature dependence incorporated from equation (10) to obtain

$$G(B,T) = k_3 m(T) B = k_3(m_{opt} - d(T_{opt} - T)^2)B = q_3(T)B \tag{13}$$

where k_3 is the kj energy equivalent of 1g of octopus tissue.

For each temperature treatment (warm or cool) and each species, a regression of body mass versus time was performed using a nonlinear mixed-effect models with an exponential model $B = Ae^{mt}$ (Fig. 3.4 and Table 3.2) in order to estimate early post-hatch growth rate m at different environmental temperatures. This standard approach for repeated measures uses maximum likelihood estimation with an underlying assumption that individual data are normal distributed to determine parameter estimates (Lindstrom and Bates 1990). For *O. ocellatus*, the regression was only performed up to the mean threshold point, after which octopus entered a slower growth phase.

Table 3.2 Feeding rate and growth parameters with associated standard errors estimated by nonlinear mixed effect models for *O, ocellatus* and *O. pallidus*.

Species	Temperature	*Feeding rate:* $\boldsymbol{F = q_1 B^{p_1}}$		*Growth:* $\boldsymbol{B = Ae^{mt}}$	
	(°C)	$q_1 \pm$ SE	$p_1 \pm$ SE	$A \pm$ SE	$m \pm$ SE
O. ocellatus	20.0	0.778±0.0402	0.46±0.0223	0.148±0.0192	0.057±0.0047
	25.0	1.117±0.1316	0.31±0.0444	0.125±0.0128	0.075±0.0039
O. pallidus	14.7	0.464±0.0300	1.206±0.1453	0.236±0.0237	0.014±0.0003
	16.9	0.517±0.0451	1.126±0.0912	0.165±0.0648	0.018±0.0073

The growth rate m was assumed to be zero at the lower and upper limit of a species' thermal range, namely 10°C and 23°C for *O. pallidus* (Stranks

1996), and 8°C and 32°C for *O. ocellatus* (Segawa, Pers. comm). For *O. pallidus*, the parameters m_{opt}, T_{opt} and d were obtained by non-linear regression of an inverted parabolic curve (eq. 10) to the combined datasets of "growth rate versus temperature" data pairs from Experiment 2 and the two "zero growth rate versus temperature" data pairs estimated from the thermal range.

For *O. ocellatus*, m_{opt} was estimated to be the maximum growth rate observed in Experiment 1 (0.075 g.day^{-1} with corresponding T_{opt} of 25°C), which resulted in an asymmetrical inverted parabolic curve for temperature-dependency (eq. 11). Parameter d_1 was obtained from non-linear regression of an inverted parabolic curve to the point pair (m_{opt}, T_{opt}) and the "zero growth rate versus temperature" data pairs (0,8) and (0,42). Parameter d_2 was obtained from non-linear regression of an inverted parabolic curve to the point pair (m_{opt},.T_{opt}) and the "zero growth rate versus temperature" data pairs (0,18) and (0,32). We assumed coefficient k_3 for both species to be the same as for *Octopus cyanea*, which was sourced from O'Dor and Wells (1987).

A plot of the temperature-dependency of growth rate for both species is represented in Fig. 3.5 below.

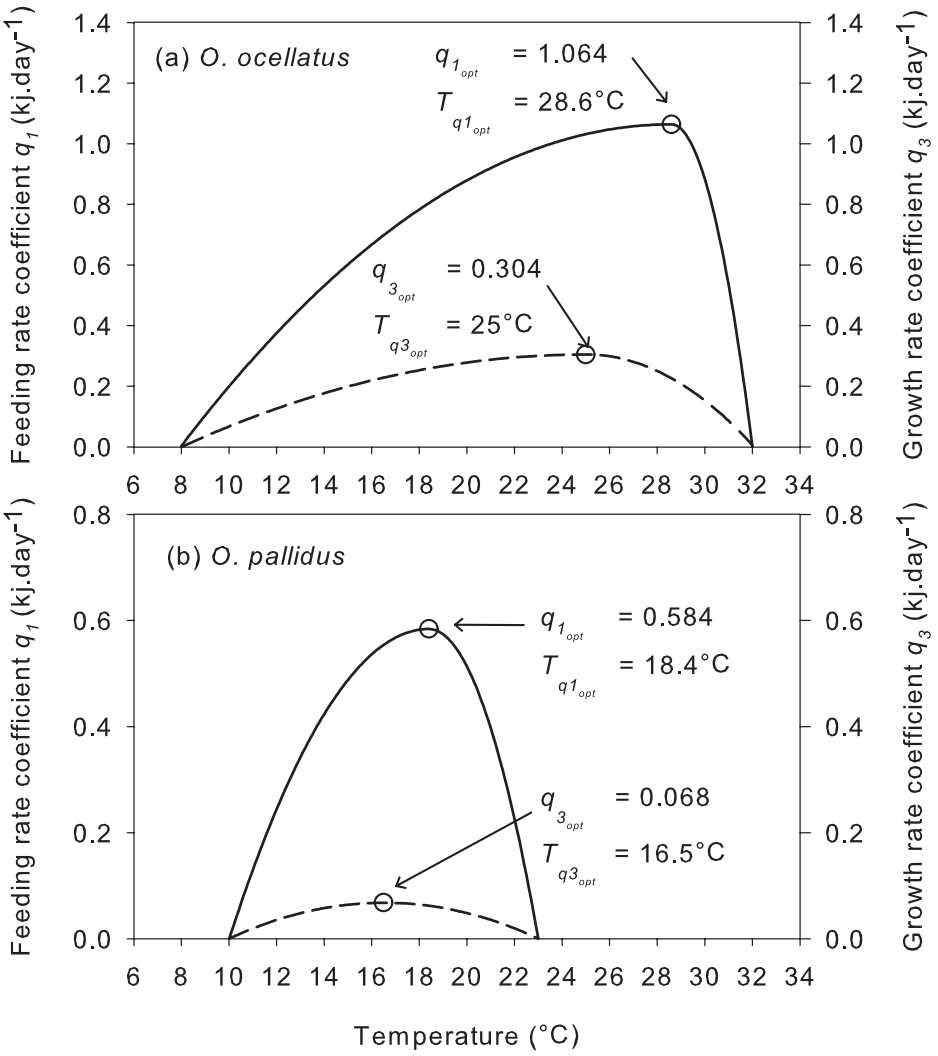

Fig. 3.5 Plots of the feeding rate coefficient q_1 (solid line) and the growth rate coefficient q_3 (dashed line) as a function of temperature T for (a) *O. ocellatus* and (b) *O. pallidus*. For each species, symmetric or asymmetric inverted parabolic curves were used to describe $q_1(T)$ and $q_3(T)$ across the thermal range in encountered in nature.

Feeding rate with $q_1(T) = f_{opt} - d_f\left(T_{f_{opt}} - T\right)^2$

From Experiments 1 and 2, individual feeding rate F (in kj.day^{-1}) were estimated every 5 to 14 days over the duration of the experiments using the formulae

$$F = F_g A_e k_f k_{w/d} \tag{14}$$

where F_g is the feeding rate in wet weight g.day^{-1}, A_e is the assimilation efficiency, k_f is the energy equivalent of the prey tissue in kj.g dry weight^{-1} and $k_{w/d}$ is the wet weight to dry weight conversion coefficient for prey tissue. For both octopus species, we used the general cephalopod A_e from Wells et al. (1983). The k_f for porcelain crabs was sourced from Perez et al. (2006) and we estimated $k_{w/d}$ from the wet weight to dry weight ratio of 30 crab samples from experiment 2. We used the values of k_f and $k_{w/d}$ estimated by McKinney et al. (2004) for the hermit crab *Pagurus longicarpus* in lieu of the other hermit crabs species (*Pagurus spp* and *Clibanarius virescens*). We performed regressions of feeding rate versus body mass using a nonlinear mixed-effect model with a power model $F(B) = q_1 B^{p_1}$ for each species and temperature treatment (warm or cool) (Fig. 3.6 and Table 3.2).

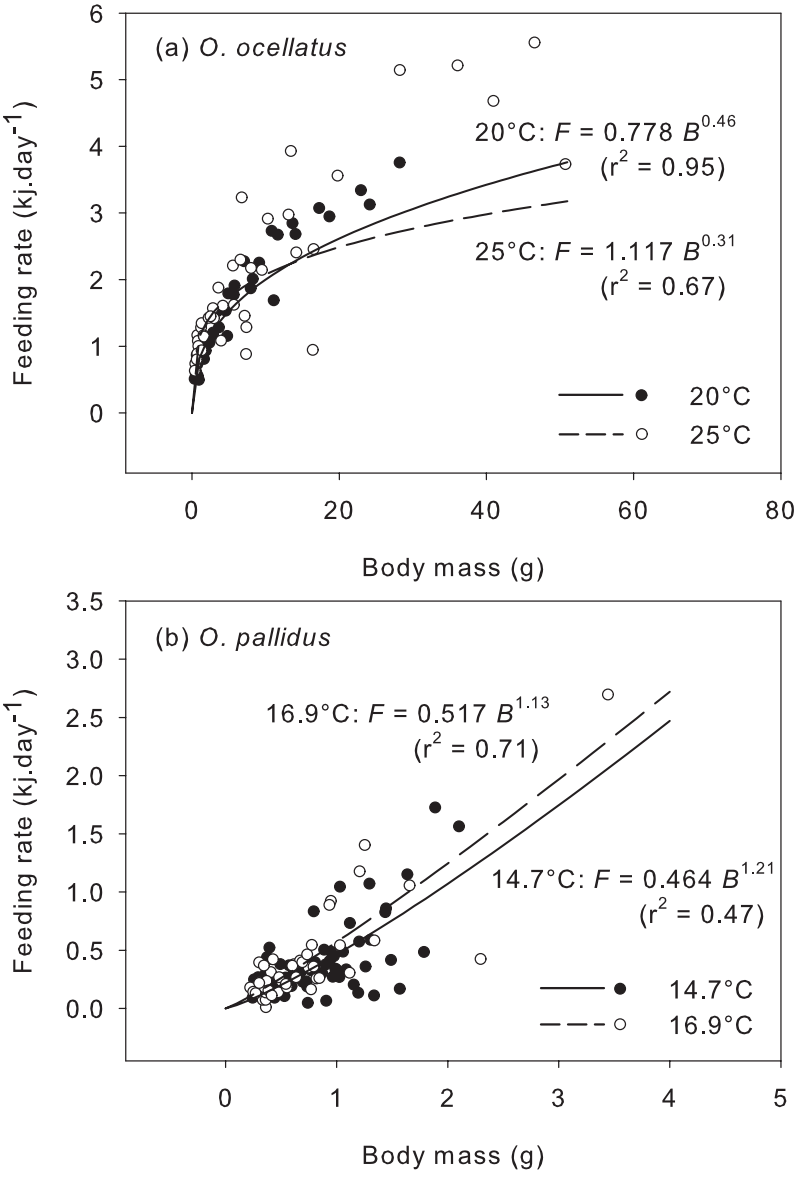

Fig. 3.6 Plots of feeding rate *F* as a function of body mass *B* estimated from nonlinear mixed effect models for a) *O. ocellatus* at 20°C (solid, *n*=5 individuals) and 25°C (dashed, *n*=5 individuals) and b) *O. pallidus* at 14.7°C (solid, *n*=4 individuals) and 16.9°C (dashed, *n*=3 individuals).

Higher temperatures result in higher feeding rates in octopus (Mangold and von Boletzky 1973; Van Heukelem 1973; Mangold 1983b; Segawa and Nomoto 2002). Towards the maximal thermal tolerance of a species

however, the feeding rate starts to decline (Mangold 1983b). The relationship between q_1 and temperature was therefore assumed to be an asymmetrical inverted parabola as for growth rate so that

$$F(B,T) = q_1(T)B^{p_1} \text{ with } q_1(T) = \begin{cases} f_{opt} - d_{f1}\left(T_{f_{opt}} - T\right)^2 & T < T_{f_{opt}} \\ f_{opt} - d_{f2}\left(T_{f_{opt}} - T\right)^2 & T > T_{f_{opt}} \end{cases} \quad (15)$$

where T_{fopt} is the optimum temperature for maximum feeding rate f_{opt}, d_{f1} and d_{f2} are constants and T is the ambient temperature. The difference between T_{opt} and T_{fopt} was assumed to be relative to the species' thermal range and proportionally constant between octopus species. Based on known thermal range and T_{opt} of the two study species and data for *Octopus vulgaris* (thermal range: 12–29°C, T_{opt} = 17.5°C, T_{fopt} = 20°C) from Aguado Giménez & García García (2002), T_{fopt} was estimated to be 28.6°C for *O. ocellatus* (thermal range: 8–32°C, T_{opt} = 25°C) and 18.4°C for *O. pallidus* (thermal range: 10–23°C, T_{opt} = 16.5°C). A non-linear regression of the inverted parabolic curve to the experimental "feeding rate versus temperature" data pairs was performed, setting the "zero feeding rate" at 8°C and 49.2°C for *O. ocellatus* and 10°C and 26.8°C for *O. pallidus*. The maximum feeding rate f_{opt} and constant d_{f1} that minimised the sum of squares to the feeding rate data were retained for each species. The constant d_{f2} was then obtained from non-linear regression of an inverted parabolic curve to the point pair (f_{opt},.T_{fopt}) and the "zero growth rate versus temperature" data pairs (0,25.2) and (0,32) for *O. ocellatus*, and (0,13.8) and (0,23) for *O.*

pallidus. A plot of the temperature-dependency of feeding rate for both species is represented in Fig. 3.5. Equations represent the general case and it is worth noting that both feeding and growth rates may be improved at lower temperatures, for example in areas subjected to upwellings (Jackson and Domeier 2003).

Metabolic rate with $q_2(T) = k_1 e^{\left(a_2 + \frac{b_2}{T+k_2}\right)}$

Temperature and body mass are the two most important factors linked to metabolic rate (Gillooly et al. 2001). Katsanevakis et al. (2005) developed a model of the form $M(B,T) = q_2(T)B^{p_2}$ to encompass the effect of both these factors on the oxygen consumption rate of *O. vulgaris*, and suggested that the term $q_2(T)$ could be generalised because metabolic rates of octopod species have a similar dependence on temperature. To obtain metabolic rate in kj.day^{-1} as a function of temperature in °C, we re-expressed the equation of Katsanevakis et al. as

$$M(B,T) = q_2(T)B^{p_2} = k_1 e^{\left(a_2 + \frac{b_2}{T+k_2}\right)} B^{p_2} \quad (16)$$

where M is the oxygen consumption rate in kj.day^{-1}, B is the body mass, T is the temperature in °C, k_1 is the conversion factor from mg.h^{-1} to kj.day^{-1}, k_2 , a_2 and b_2 are constants, and p_2 is a species specific metabolic rate exponent. Parameter values for a_2 and b_2 were imported from Katsanevakis et al. (2005). Values for p_2 were estimated from Experiment 1 for *O. ocellatus* and Experiment 3 for *O. pallidus*. Coefficients k_1 and k_2 were obtained from the literature (Prosser 1973, Elliot & Davison 1975). Since

the original formulae was tested in the temperature range 13°C to 28°C (Katsanevakis et al. 2005), the function $q_2(T)$ was determined across the temperature ranges 13°C to 28°C for *O. ocellatus*, and 13°C to 23°C for *O. pallidus* to avoid extrapolation.

Model estimation of transition body mass and age

The threshold body mass B^* and age t^* estimated experimentally were compared with model growth projections for B^* and t^* at the experimental rearing temperatures of 20°C and 25°C for *O. ocellatus*, and at 14.7°C and 16.9°C for *O. pallidus*.

The relationship between growth pattern and temperature was explored by plotting B^* and t^* as functions of temperature between the ranges of 13°C and 23°C for *O. pallidus* and 13°C and 28°C for *O. ocellatus*. Additionally, growth trajectories over 100 days were projected with individuals starting from the same hatchling size A, but experiencing different temperature scenarios. Growth trajectories were estimated every degree between 13°C and 28°C for *O. ocellatus*, and 13°C and 23°C for *O. pallidus*. In this simple simulation, growth was assumed to be exponential in form until the transition point. The second slower growth phase was represented as linear and tangential to transition point (t^*, B^*). Hatchling size A was representative of the species and was set to 0.11g for *O. ocellatus* (Segawa and Nomoto 2002) and 0.25g for *O. pallidus* (Leporati et al. 2007).

Sensitivity analysis

A sensitivity analysis was performed to assess the response of model growth projections to small changes in parameter values. The metric of "elasticity" was used, in which the effect of proportional (rather than absolute) perturbations on a given output quantity are evaluated (Caswell 2001). Elasticity is defined as

$$E_p = \frac{X_p - X_0}{X_0} \times 100 \qquad (17)$$

where E_p (%) is the elasticity of the output quantity to a given % increase in parameter p, X_0 is the output of the original model, and X_p is the output of the model modified for parameter p (Barbeau and Caswell 1999; Lauzon-Guay et al. 2006). Elasticities of B^* (critical transition weight) and t^* (critical transition age) to independent perturbations of d_f, T_{fopt}, f_{opt}, p_1 a_2, b_2, p_2, d, T_{opt} and m_{opt} were calculated at two levels of parameter change, namely at 1% and 5%. To assess the influence of temperature, the analyses were repeated at four temperatures across the species thermal range, namely at 15°C, 20°C, 25°C and 28°C for *O. ocellatus*, and at 13°C, 16°C, 18°C and 21°C for *O. pallidus.*

RESULTS

Estimation of transition body mass and age

For both species, there was reasonable agreement between the laboratory observations and the projections of the model (Table 3.3).

Table 3.3 Comparison of observed (obs.) with simulated (sim.) transition body mass *B** and transition age *t** for *O. ocellatus* and *O. pallidus*.

Species	Temperature (°C)	*B** obs.± 95% C.I. (g)	*B** sim. (g)	*t** obs.± 95% C.I. (days)	*t** sim. (days)
O. ocellatus	20.0	2.5 ± 3.5	5.3	43 ± 27	56.6
	25.0	2.3 ± 1.6	5.6	37 ± 12	52.4
O. pallidus	14.7	no threshold	no threshold	no threshold	no threshold
	16.9	no threshold	no threshold	no threshold	no threshold

Model estimates for *B** and *t** for *O. ocellatus* were close to the observed values (Table 3.3), encompassed within the 95% C.I. at 20°C and slighly above the 95% C.I. at 25°C. *Octopus pallidus* did not display a two-phase growth pattern during the 143 days of the experiment and the model predicted that exponential growth would always be supported at the temperatures tested (Table 3.3). Hence, only results for *O. ocellatus* are presented for the remaining analyses.

Impact of temperature on growth pattern

The relationships between temperature and threshold size, and temperature and threshold age, were not linear. As temperature increases, *B** is projected to slowly increase while *t** is projected to decrease, so that the transition out of exponential growth would occur at an earlier age but similar body mass (Fig. 3.7). Beyond 25°C however, *B** and *t** are both

projected to increase so that the transition from exponential growth would be expected to occur later and at higher body mass.

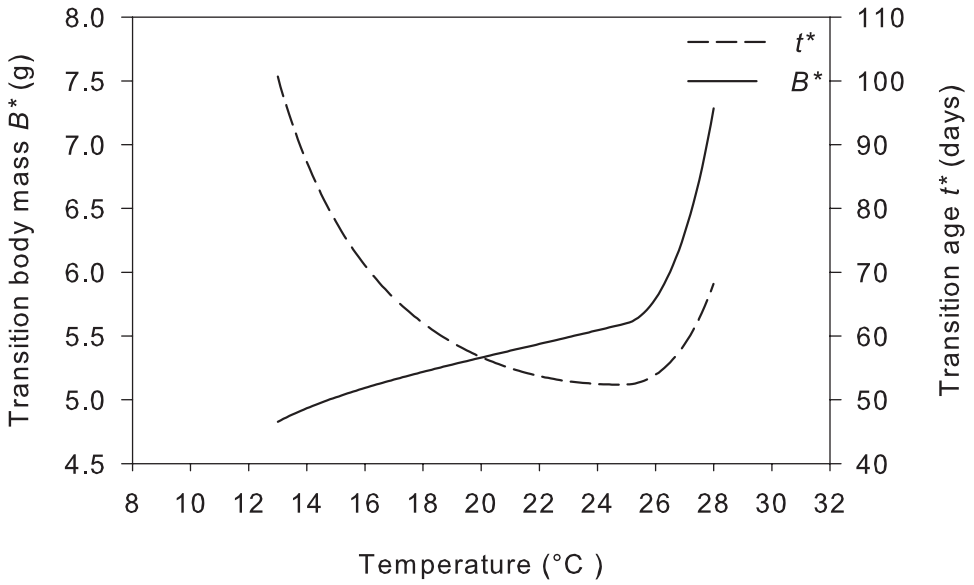

Fig. 3.7 Plot of the model threshold body mass B^* and transition age t^* as a function of environmental temperature T for *O. ocellatus*.

Projected growth trajectories suggested that higher temperatures do not necessarily translate to higher body mass, with individuals growing at 23°C reaching higher body mass at 100 days than those at 28°C (Fig. 3.8). Projections at temperatures between 23°C and 26°C produced the largest individuals. A 1°C change in environmental temperature produced a 1% to 15.5% difference in B^* and 0.1% to 16.2% in t^*, which resulted in a 0.7% to 62.6% difference in body mass at the end of the simulation. Simulation at 13°C suggested that exponential growth would always be sustained in the first 100 days.

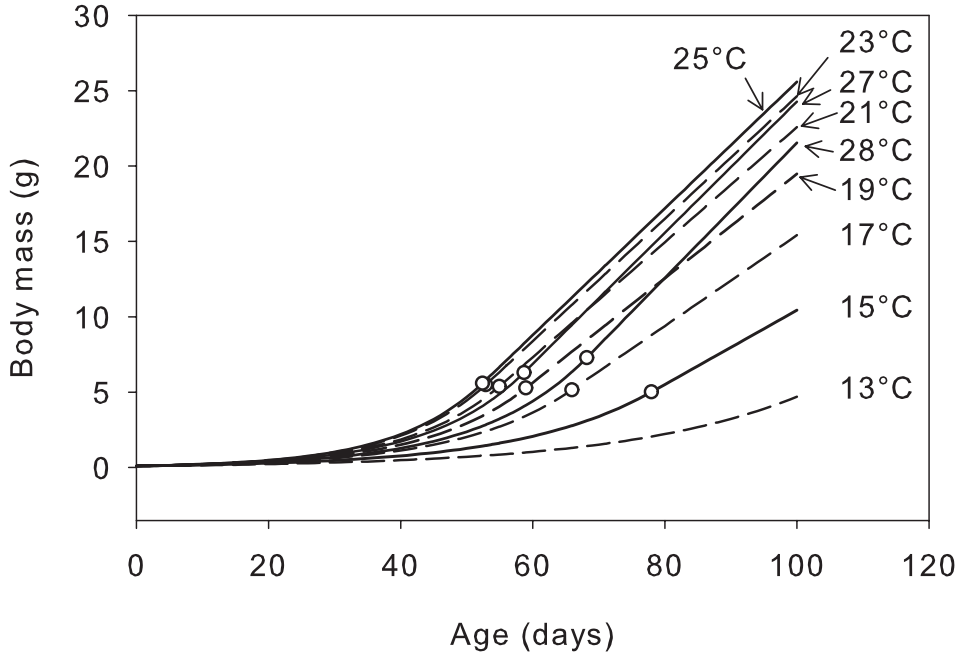

Fig. 3.8 Projected growth trajectories at selected environmental temperatures for *O. ocellatus.* Circles indicate the transition point (*t**, *B**) for each individual.

Model sensitivity

Results from the sensitivity analyses performed with either ±1% and ±5% parameter changes were qualitatively similar and hence for conciseness only the sensitivity analyses for a 1% increase are presented (Fig. 3.9).

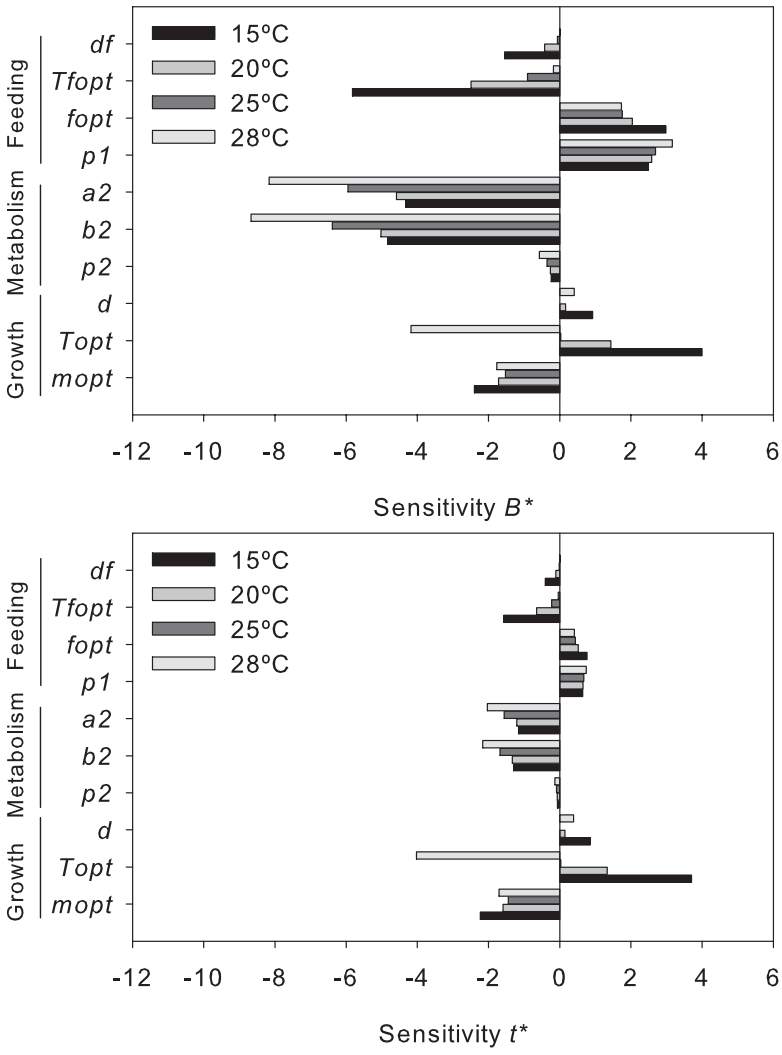

Fig. 3.9. Elasticity to small perturbations in feeding (F_{opt}, T_{opt}, d_f), metabolism (a_2, b_2, p_2) and growth (m_{opt}, T_{opt}, d) rate parameters of a) B^* and b) t^* at 15°C, 20°C, 25°C and 28°C for *O. ocellatus*.

The threshold body mass B^* was most sensitive to increases imposed on metabolic rate parameters, in particular to changes in b_2 and a_2. The corresponding transition age t^* exhibited a similar sensitivity profile. Temperature had the most effect on the sensitivity of B^* to changes in the feeding parameter T_{fopt} and growth parameter T_{opt}. The sensitivity of B^* to

changes in metabolic parameters (and most feeding parameters) also increased with temperature, and was more pronounced at temperatures in the upper thermal range of the species. The sensitivity profile of transition age t^* was similar to that of B^* but was less influenced by temperature.

DISCUSSION

The energy balance paradigm reflected appropriately the conditions experienced by the animals and the growth pattern of both species, providing realistic estimations of the transition mass B^* and transition age t^* when two-phase growth was detected experimentally. Results reinforce the hypothesis advanced by Forsythe (1993) that changes in environmental temperature as small as 1°C can have significant effect on cephalopod growth. A 1°C increase in temperature in the model implied up to 15.5% change in the threshold body mass for *O. ocellatus* and considerably altered the growth trajectory of individuals.

The model suggests that the influence of temperature on threshold body mass B^*, and hence on the shape of individual growth curves, would be mostly driven by metabolism. Sensitivity analyses indicate metabolic rate is the most influential component of the model and will generally more acutely influence threshold body mass rather than threshold age, as also reported for *Sepia apama* with the basic energy balance model (Grist and Jackson 2004). More significantly, analyses suggest that elevated

temperature would increase the sensitivity of B^* to changes in metabolic rate, which would have important ramifications on the structure of cephalopod populations in the coming decades. The predicted increase in seawater temperature combined with a reduction in seawater pH, due to increasing CO_2 levels in the oceans, will decrease the ability of cephalopods to bind oxygen for transport (Seibel and Fabry 2003), therefore altering metabolic rate at the individual level. This would impact on the body mass at transition out of exponential growth, possibly affecting size at maturity, and is likely to substantially alter the population dynamics of most cephalopod species. As mentioned previously, octopus are less sensitive than squids to decrease in seawater pH and the extend to which octopus populations would be affected mostly depends on the level of seawater acidification. If the case of *Octopus dofleini* (Miller and Mangum 1988) is to be generalised to all Octopods, an acidification of seawater to a pH of 7.2 or less would be required to affect blood oxygen saturation, and hence metabolism.

The reversal in the decreasing trend of t^* observed in model projections at higher temperatures is connected to the optimal temperature for growth T_{opt}. As temperature increases beyond that point, more energy becomes available from food while overall energy expenditure starts to decrease due to a decline in growth rate, hence delaying both the threshold time and body mass, at least until the optimal temperature for feeding T_{fopt} is

reached. The accurate estimation of T_{opt} and T_{fopt} is therefore crucial for these type of energetic models, but these data are sparse for octopus.

Currently, the lack of a complete range of data on feeding, metabolism and growth for cephalopod species is impeding, and models such as the one presented here require drawing parameters from a wide range of species. The estimated transition point being just above the 95% C.I. at 25°C for *O. ocellatus* probably reflects these unavoidable approximations, and there is a need for concerted efforts to conduct the full range observations on some species well suited to studies in captivity and representative of major fished species. There is also a need to establish whether temperature affects the metabolic rate and feeding rate exponents p_1 and p_2 for more species than just *O. vulgaris* (Katsanevakis et al. 2005). These exponents are considered temperature-independent in the present analysis, but one or both of these parameters could vary with temperature with implication for size or age at transition out of exponential growth.

Energetic information on wild cephalopods is notoriously difficult to obtain. Average growth rate (Pecl 2004; Leporati et al. 2008b) and aspects of metabolism (O'Dor et al. 1994; Webber et al. 2000; O'Dor 2002; Aitken et al. 2005) have successfully been estimated for a few species, but feeding data remains largely inaccessible. Carefully conducted laboratory studies with animals fed ad libitum and subject to minimal human interaction, as was the case for *O. ocellatus*, are thought to be representative of feeding

and growth rates of wild animals (Wells and Clarke 1996), and remain the only option to fully parameterise energetics models for wild cephalopods. Field studies may never elucidate whether or not cephalopods demonstrate a two-phase growth pattern in the wild. Growth curves that adequately represent the behaviour of a population mean can very poorly describe the pattern followed by any individual in that population (Alford and Jackson 1993). Furthermore, while statolith (Jackson 1990) and stylet increment analyses (Doubleday et al. 2006; Leporati et al. 2008b) provide insights into individual growth rate integrated over the life span, the lack of a relationship between increment width and daily growth rate (Jackson and Moltschaniwskyj 2001) renders the detection of a change in growth difficult and the re-construction of individual growth curves impossible (Arkhipkin 2005). This study suggests that a transition out of exponential growth is not a compulsory phase, it may occur late, as seen for *O. ocellatus* at lower temperatures, or not at all, as seen for *O. pallidus*.

CONCLUSION

The model presented in this chapter is the first to include both body size and temperature-dependency in the overall energy budget of cephalopods and is adaptable to both squid and cuttlefish species. It emerges from the simulations that metabolism is the main driver of the shape of the growth curve, through the influence of metabolic rate on the energy balance and its subsequent impact on the threshold body mass B^*. This model also

suggests that two-phase growth may not always occur and that animals could remain in exponential growth under certain conditions. Using bioenergetics, this representation captured the environmentally induced plasticity in growth characteristic of cephalopods. The incorporation of periodic variation in temperature to simulate seasonal water temperature as well as individual variability in growth would provide a better representation of the individual growth trajectories and give insights into size-at-age variation in natural populations This is the focus of the next chapter.

Ch 4

Modeling size at age in wild immature octopus: the relative influence of the principal abiotic and biotic factors

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ABSTRACT

The population dynamics of cephalopods are poorly understood because intra-specific size-at-age is characteristically variable. Much of the variation observed is attributed to temperature and food, but other generally overlooked factors such as hatchling size and inherent growth capacities also affect size-at-age. In this chapter, the relative influence of the principal abiotic (environmental temperature) and biotic (hatchling size, inherent growth capacity, food consumption) factors affecting size-at-age in immature octopus is investigated. Using a bioenergetics model and size-at-age data of wild-caught immature *O. pallidus*, the juvenile growth trajectories of individuals hatched in different seasons (summer, autumn and winter) is simulated based on food availability, metabolism, environmental temperature and individual variability, under an assumption of two-phase growth. Simulations predict that the effect of hatchling size on size-at-age was secondary to that of inherent growth capacity. Projections suggest that wild immature populations comprise a mixture of individuals displaying exponential growth and two-phase growth, and that the proportion of each depends primarily on individuals' inherent growth capacities and food availability. High food intake was projected to decrease the number of individuals displaying two-phase growth by delaying the transition between the two growth phases, resulting in larger individuals. Overall, individuals hatched in summer grew to larger sizes and matured earlier than individuals hatched in autumn or winter, independent of food availability. The size-at-age distribution of the summer and autumn cohorts tended to become bimodal under certain food intake levels, which highlights the importance of coupling size data with accurate age estimates in future octopus population studies.

INTRODUCTION

Individual variability in growth has been observed in many taxa, including cephalopods (Domain et al. 2000), gastropods (Hughes and Roberts 1980) and teleosts (Searcy and Sponaugle 2000), resulting in intra-specific size-at-age data often being highly variable (Challier et al. 2006a). Under these conditions, understanding population dynamics and changes in population size-structure becomes challenging (Gurney and Veitch 2007). In cephalopods, growth rates are mainly governed by nutrition, body size, water temperature and, later in the life cycle, the energy diverted towards reproduction (Semmens et al. 2004). Both the quantity (Jackson and Moltschaniwskyj 2001; Villanueva et al. 2002) and quality (Segawa 1990; Iglesias et al. 2004) of food influence growth, with prey high in protein and low in lipid providing the highest growth rates (Segawa 1993; Lee 1994; García García and Aguado Giménez 2002). Water temperature is also of critical importance in defining cephalopod developmental rates and there has been much emphasis on examining the effects of temperature on growth, and its implications for size-at-age (see Forsythe and Van Heukelem 1987; Forsythe 2004; and Semmens et al. 2004 for a review). A key hypothesis that emerged from this research is the "Forsythe Effect" (Forsythe 1993; Forsythe 2004), which states that when hatching occurs over a period of continually warming days (and hence warming water temperatures), each micro-cohort of hatchlings will grow significantly faster than micro-cohorst(s) hatched only weeks previously.

This hypothesis is supported by evidence from both laboratory (Villanueva 2000; Hatfield et al. 2001; Leporati et al. 2007) and field studies (Jackson et al. 1997; Hatfield 2000; Jackson and Moltschaniwskyj 2002), making seasonal temperature, alongside nutrition, the two most important factors contributing to variations in size-at-age in natural populations.

Other generally overlooked factors such as hatchling size (Pecl et al. 2004b; Leporati et al. 2007) can also affect size-at-age. Within a species, hatchling size is known to vary by at least 147% in squid (e.g. Sepioteuthis australis, Pecl et al. 2004b) and 239% in cuttlefish (e.g. *Sepia officinalis*, Domingues et al. 2001). Given that most cephalopods are believed to follow a two-phase growth pattern, differences between individuals at hatching can amplify throughout the lifespan (Pecl et al. 2004b) and impact on size-at-age. Hatchling size variation has multiple origins that can be divided into environmental effects, maternal effects and genetic effects. The direct effect of temperature on hatchling size is well known (Boletzky 1994), with higher incubation temperatures resulting in faster embryonic development and hence smaller hatchlings, and conversely lower incubation temperatures resulting in slower development and larger hatchlings. Maternal condition during oogenesis can also introduce variation in intra-specific hatchling size as hatchling size is positively correlated with maternal nutrition in several species (e.g. *Octopus vulgaris*, Sakaguchi et al. 2002; *Euprymna tasmanica*, Steer et al. 2004). Genetic differences may also be a source of hatchling size variation. Multiple

paternity within broods has been demonstrated for some cuttlefish (Naud et al. 2004) and squid species (Shaw and Boyle 1997; Buresch et al. 2001), and differences in paternity has been linked to a difference in hatchling size (*Loligo forbesi*, Emery et al. 2001).

Another potential source of individual variability in size-at-age is inherent growth plasticity (Forsythe and Van Heukelem 1987; Boyle and von Boletzky 1996). Genotype is known to have a significant effect on physiological rates in molluscs, particularly on growth rates (Koehn 1991). Phenotypic plasticity, where a single genotype produces different phenotypes as a result of environmental conditions, also appears to play an important role in the variability observed in cephalopods (Boyle and von Boletzky 1996).

Different combinations of the above factors imply that size-at-age distributions for a given population can vary among micro-cohorts and years, and consequently alter the overall population fecundity, which is largely determined by adult size in cephalopods (Mangold 1987). This is especially significant for species that have no overlapping generations and are commercially exploited, because population size and structure in any given year is a direct function of the success of breeding and recruitment from the previous year (Caddy 1983). This can lead to large inter-annual changes in abundance and render the population less likely to recover from overfishing, given the lack of multiple generations to compensate for

low recruitment in any specific year.

Evaluating the relative influence of the many factors affecting size-at-age would require a precise knowledge of the various conditions experienced by individuals during their life history, such as quantity and quality of food consumed or the exact environmental temperatures experienced at each life stage. Obtaining specific growth information for individual animals in the wild is difficult and although there has been progress with some species through tagging (Jackson et al. 2005a), the low levels of tag retention, short lifespans and high natural mortality reducing recapture rates remains problematic (Boyle and Rodhouse 2005). An increasing number of studies attempt to link the biology of cephalopods to their physical environment in nature (Lefkaditou et al. 2008; Pierce et al. 2008; Sanchez et al. 2008). Some studies have focused on growth and size-at-age in natural populations in relation to Sea Surface Temperature (SST) (Hatfield 2000; Ichii et al. 2004; Pecl et al. 2004a) but due to the lack of information, no other factors affecting size-at-age were taken into consideration. Controlled culture experiments provide some indication of the relative impact of different growth determinants (Forsythe and Hanlon 1988; Segawa and Nomoto 2002; Leporati et al. 2007) and remain invaluable to investigations of environmental influences on cephalopod life history. However, captivity can introduce biases and alter the actual processes of growth in cephalopods (Pecl and Moltschaniwskyj 1999).

Moreover, changes in temperatures lead to large changes in growth rates and size-at-age (Forsythe et al. 2001b; Hatfield et al. 2001), yet most experiments have used static temperature regimes which do not reflect the seasonal temperature variations encountered in nature.

The purpose of this chapter was to use a modelling approach to investigate the relative influence of the principal abiotic (environmental temperature) and biotic factors (hatching size, inherent growth capacity, food consumption) affecting size-at-age in immature octopus. This method represents a complementary approach to both field and laboratory studies as it allows an investigation into the impact of factors such as food consumption in natural populations, which would otherwise not be possible. Using the model developed in the previous chapter, an individual-based bioenergetics model was generated, which determined the growth trajectories of individuals hatched in different seasons based on food availability, metabolism, environmental temperature, and individual variability (i.e. hatchling size and inherent growth capacity). The model was parameterized from a combination of laboratory and field data and was validated against size-at-age data of wild individuals. The level of individual variability in growth and food intake necessary to encompass the variation in size-at-age observed in our sample was determined. The relative influence of individual variability and food availability on size-at-age, as well as the impact of food availability on the

percentage of individuals displaying two-phase growth and the age and size at the onset of sexual maturation were assessed. Given reproductive growth in octopus differs between sexes in both energy allocation and timing (Semmens et al. 2004), the analysis was limited to size-at-age in immature animals on the grounds of model parsimony. In addition, as no immature males were caught during the 2 years of sampling (Leporati et al. 2008a), the model focused on females only.

MATERIALS AND METHODS

Dataset

A total of 409 female *O. pallidus* were collected between 2004 and 2006 using a bottom set long line of octopus pots set at 26 m depth in Bass Strait waters, Tasmania, Australia (40º43.342 S and 145 º20.060 E) (see Leporati et al. 2008a for details of the sampling regime). Individuals were weighed, aged via daily increments in the stylet (Leporati et al. 2008b), sexed and their reproductive status assessed (Leporati et al. 2008a). For the purpose of this chapter, we selected all immature females hatched in January (n=12), May (n=12) and July (n=18) 2005 to represent cohorts hatched in (austral) summer, autumn and winter respectively. The dataset contained too few immature females hatched in spring 2005 for that seasonal cohort to be represented in our simulations. Gear selectivity and the large numbers of micro-cohorts within a year contributed to the low number of suitable data points. While it is a possibility that a larger sample of

individuals would have expressed an even greater variability, the sample sizes were nevertheless deemed sufficient to represent the range of size-at-age attainable in the wild given the high individual variability present in octopus.

Model development

The basis of the model was the temperature-dependent energy balance model (TEBM) described in chapter 3, which determines the shape and duration of the exponential growth phase in female octopus. The modified version presented in this chapter, the dynamic temperature-dependent energy balance model (DTEBM), allows the growth pattern of wild octopus hatched in different seasons to be simulated by adding the second growth phase, individual variability and dynamic temperatures to the original TEBM. Reproductive growth was not included in the model because we are concerned with immature individuals only. Fig. 4.1 synthesizes the modeling approach used for this model.

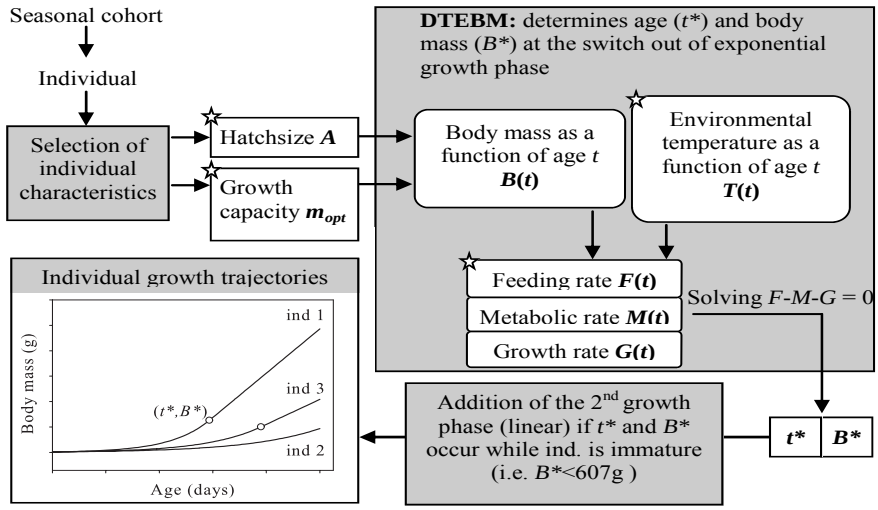


Fig. 4.1 Schematic representation of the modeling approach used to estimate individual growth trajectories. The purpose of the model was to investigate the relative influence of environmental temperature, food consumption, hatching size and inherent growth capacity (marked with a star) on size-at-age in immature octopus.

The DTEBM and the estimation of the exponential growth phase

Whereas the energy balance model described in chapter 3 describes growth at a fixed temperature, the DTEBM presented here incorporates temperature dependence which enables growth to be described under a seasonally fluctuating temperature environment (see Table 4.1 for description and values of DTEBM terms). A standard sinusoidal temperature function

$$(t + t_{hatch})\,T = T_0 + T_1 \cos k\left(t + t_{hatch} + c\right) \qquad (18)$$

was used to represent seasonal environmental temperature T as a function of time of the year where t is the age of the individual (in days), t_{hatch} is the hatching day in a 365 day year, T_0 is the mean annual temperature

(baseline), T_1 is the annual fluctuation of temperature around T_0 (amplitude), k is the frequency and c is the time lag necessary to align the maximum of the curve to the occurrence of the maximum temperature in a year (shift). Temperature parameters were determined from SST data for the years 2005/06 downloaded from the National Oceanic and Atmospheric Administration (NOAA) USA web page (www.noaa.gov).

Body mass is traditionally expressed as

$$B(t) = Ae^{mt} \tag{19}$$

where t is the post-hatch age, A is the hatchling size and m the fixed growth rate (in day^{-1}). However, the growth rate coefficient m in this model is temperature-dependent, so that body mass is now given by:

$$B(t) = Ae^{I(t)} \qquad \text{where } I(t) = \int m(t)dt \tag{20}$$

and $m(t) = m_{opt} - d(T_{opt} - T)^2$

$$= m_{opt} - d(T_{opt} - (T_0 + T_1 \cos k(t + t_{hatch} + c)))^2 \tag{21}$$

By incorporation $B(t)$ and $T(t)$ in Eq. (8) (from chapter 3), we obtain

$$E(t) = F(t) - M(t) - G(t) \tag{22}$$

where

$F(t) = q_1(T(t))B(t)^{p_1}$
$M(t) = q_2(T(t))B(t)^{p_2}$
$G(t) = q_3(T(t))B(t)$

Table 4.1 Equations and parameter values for the dynamic temperature-dependent energy balance model (DTEBM). A is the hatchling size, t is the age (in days) and t_{hatch} the hatching day in a 365 day year.

Eq no	Equations and parameters	Values
(13)	**Growth rate *G*:** $q_3 B$ **with q3= with** $q_3 = k_3\left(m_{opt} - d\left(T_{opt} - T\right)^2\right)$	
	Optimum temperature for growth (T_{opt}) (in °C)	16.5
	Growth rate coefficient at T_{opt} (m_{opt}) (in day^{-1})	0.0217 to 0.0967
	Parabolic constant (d)	5.14 10^{-4} to 2.3 10^{-3}
	Energy equivalent of octopus tissue (k_3) (in kj.g^{-1})	4.05848
(15)	**Feeding rate *F*:** $q_1 B^{p_1}$ with $q_1 = f_{opt} - d_f\left(T_{fopt} - T\right)^2$	
	Optimum temperature for feeding (T_{fopt}) (in °C)	18.4
	Feeding rate at T_{fopt} (f_{opt}) (in kj.day^{-1})	2.044
	Parabolic constant (d_f) if $T \leq T_{fopt}$	0.029
	$T > T_{fopt}$	0.0966
	Feeding rate exponent (p_1)	0.75
(16)	**Metabolic rate *M*:** $q_2 B^{p_2}$ **with** $q_2 = k_1 e^{\left(a_2 + \frac{b_2}{T + k_2}\right)}$	
	Metabolic rate exponent (p_2)	0.88
	Conversion factor O_2 mg.h^{-1} to kj. day^{-1} (k_1)	0.33758
	Conversion factor °K to °C (k_2)	273.15
	Constant (a_2)	21.80
	Constant (b_2)	-6952.8
(18)	**Temperature *T*:** $T_0 + T_1 \cos\left(k\left(t + t_{hatch} + c\right)\right)$	
	Baseline (T_0)	15.06
	Amplitude (T_1)	2.83
	Frequency (k)	2*pi/365
	Shift (c)	-73
(20)	**Body mass *B*:** $Ae^{\int_0^t m(t)}$	

As per chapter 3, the post hatch age and body mass at which the exponential growth phase terminates in an individual were defined as t^* and B^* respectively. Using eq. (22), an iterative search was conducted for the threshold age t^* which achieves $E(t)=0$. The corresponding body mass B^* was calculated according to

$$B^* = B(t^*) = Ae^{I(t^*)} \text{ where } I(t^*) = \int_0^{t^*} m(t)dt \quad (23)$$

Food consumption in wild octopus

From chapter 3, the optimum temperature for maximum feeding T_{fopt} in *O. pallidus* was estimated at 18.4°C, the corresponding f_{opt} was estimated at 0.584 (kj.day^{-1}) and the feeding rate exponent p_1 at 1.17. Animals reared in the laboratory are held in an impoverished environment with limitations on food choice, tactile and visual stimuli as well as restricted space. These factors may lead to suboptimal feeding (Houlihan et al. 1998) and it is reasonable to assume that the f_{opt} value would be higher in the wild. Moreover, a value of $p_1>1$ signifies that individuals always have enough energy intake to cover growth and metabolic costs, which is unlikely to be the case for animals in nature. A range of f_{opt} and p_1 values were therefore tested to identify plausible estimates for wild animals. A range of values was explored for p_1, from 0.40 to 1 in 0.05 increments, based on the lowest p_1 value of 0.39 described for an octopus species (*Octopus ocellatus*, see Ch.3). For f_{opt}, values up to 4 times the f_{opt} value found in the laboratory were

tested, corresponding to a range of values from 0.584 to 2.336 in increments of 0.292. Values above 2.336 ($kj.day^{-1}$), equivalent to a food consumption in excess of 1 g of crab flesh per day (according to values of O'Dor and Wells 1987) for a 0.3 g hatchling, were deemed too high for juveniles of this species.

Individual variability

We introduced individual variability at two levels: (1) variation in hatchling size (parameter *A* in eq. 19), and (2) variation in inherent growth capacities (parameter m_{opt} in eq. 21). Variation in inherent growth capacity and variation in hatchling size were assumed to act independently.

Hatchling size varies both within a cohort (intra-cohort variation) and between seasons (inter-cohort variation) (Pecl et al. 2004b). The model was parameterized with three seasonal distributions, namely a summer, autumn and winter distribution for hatchling size, from which individuals were randomly selected. To do this, the population variability in hatchling size was first estimated from data obtained for 58 individuals hatched in winter (June) 2005 from a single brood originating from Bass Strait waters and maintained at ambient temperature in the laboratory (Leporati et al. 2007). The June hatch distribution followed a log-normal distribution (Fig. 4.2d) and was used as a template for the summer and autumn seasonal

hatchling size distributions (Fig. 4.2a-c), based on the following assumptions:

• The mean of the hatching size distribution is a function of incubation duration.

• While incubation duration in days varies with environmental temperature (Boletzky 1994), incubation duration in degree-days remains constant independent of the season. Incubation in degree-days (*icubdd*) was calculated according to

$$incubdd = \sum_{1}^{incubdays} \left(dailytemp - T_{null} \right) \quad (24)$$

where *incubdays* is the observed number of days of incubation for the June cohort, *dailytemp* is the daily temperature and T_{null} is the threshold development temperature for *O. pallidus* eggs. Based on a threshold development temperature of 8ºC, an observed *incubdays* of 150 days and known environmental temperature records from both Bass Strait (NOAA) and the laboratory, the incubation period was estimated to be 1067.5 degree-days.

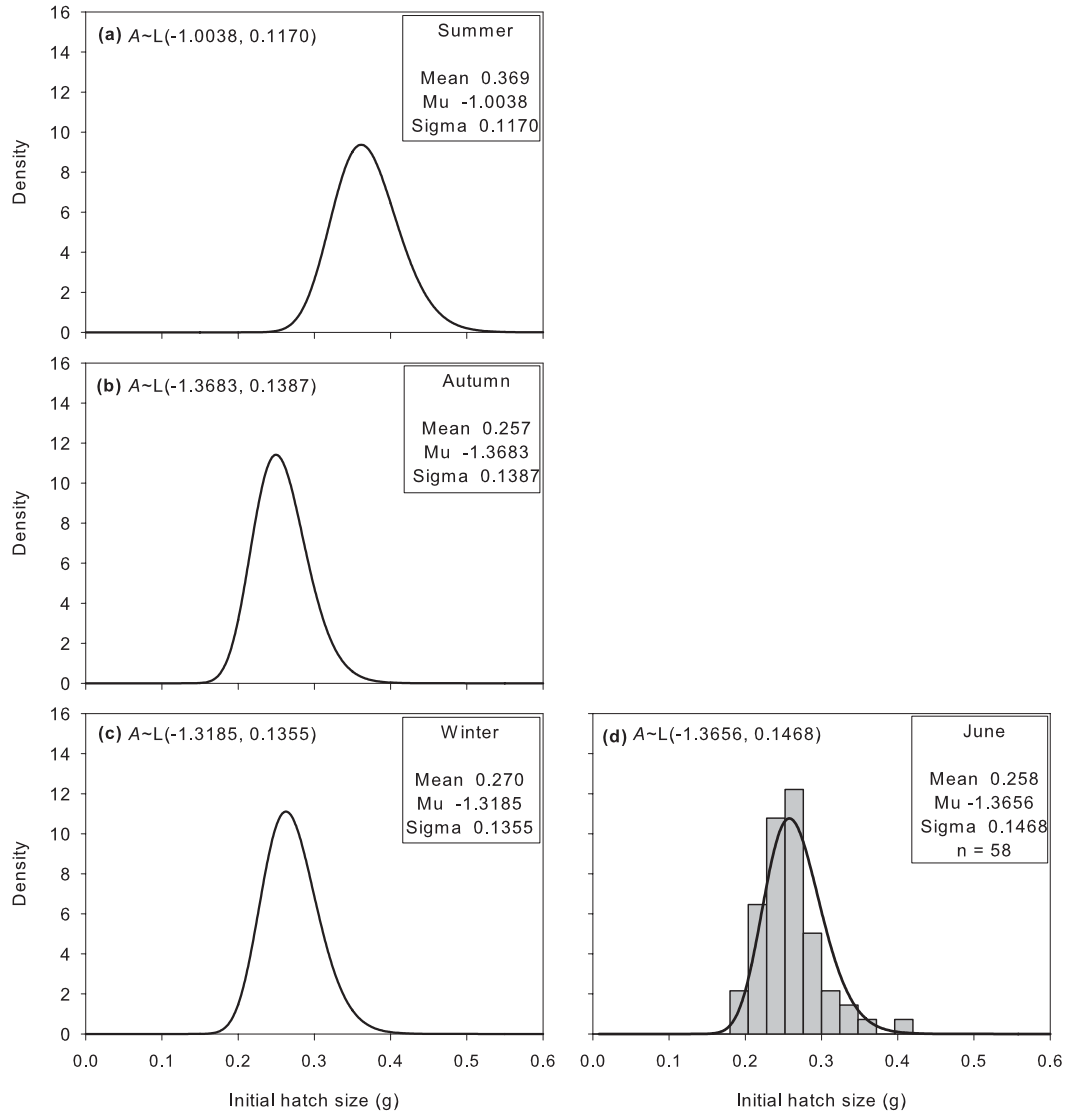


Fig. 4.2 Hatchling size distribution used in the model for *Octopus pallidus* in a) summer, b) autumn and c) winter. The distributions were estimated statistically (see Materials and Methods section) and were described by a lognormal distribution $A \sim \mathrm{L}(\mu, \sigma)$ where $\mu = \ln(m)$ and m is the median of the distribution. Plot d) shows the estimated and observed June hatchling size distribution.

• The relationship between the mean of the initial hatchling size distributions and incubation time (in days) is positively linear (Fig. 4.3a). Based on the incubation duration in degree-days, and assuming hatching on the 1st day of the month, the incubation duration (in days) was calculated for each monthly cohort using NOAA temperatures from the Bass Strait region (Table 4.2). We assumed the mean of the June hatchling size distribution to be that of the experimental brood (i.e. 0.258g) and the proportional change in mean hatchling size to be 0.5% per additional incubation day. This was based on an observed change in hatchling size of 25% for a 48 day difference in incubation duration between the summer and autumn cohorts in *Sepiotheuthis australis* (Pecl et al. 2004b), a species with similar thermal range and hatchling size.

• The relationship between mean and variance of the initial hatchling size distributions is positively linear (Fig. 4.3b).

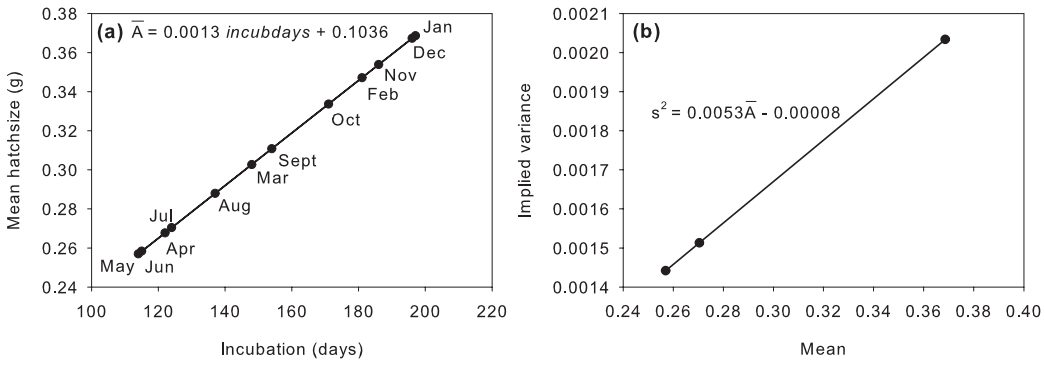


Fig. 4.3 Estimation of seasonal hatchling size distributions parameters: a) Relationship between incubation time (*incubdays*) and mean of the hatchling size distribution ($\bar{A}$), b) Relationship between mean hatchling size ($\bar{A}$) and variance (s^2) used to estimate the summer, autumn and winter hatchling size distributions.

Table 4.2 Predicted incubation time in Bass Strait waters (based on an incubation duration of 1067.5 degree-days) and mean of the hatchling size distribution for *O. pallidus.* The (*) represent observed data for pale octopus.

Hatch month	Incubation (days)	Mean hatchling size (g)
January	197	0.369
February	181	0.347
March	148	0.303
April	122	0.268
May	114	0.257
June	115	0.258 (*)
July	124	0.270
August	137	0.288
September	154	0.311
October	171	0.334
November	186	0.354
December	196	0.367

Inherent individual variability (both genotypic and phenotypic) was incorporated in the model via the parameter m_{opt} by assigning a specific "growth potential" to each individual during the first (exponential) phase of growth before the start of the simulation. A normal distribution was considered but failed to provide acceptable results. In the absence of information to the contrary, a uniform distribution was chosen. Values for the parameter m_{opt} were randomly selected from a uniform distribution $m_{opt} \sim U[min\_m_{opt}, max\_m_{opt}]$, resulting in a different growth rate coefficient $m(t)$ for each individual (Fig. 4.4).

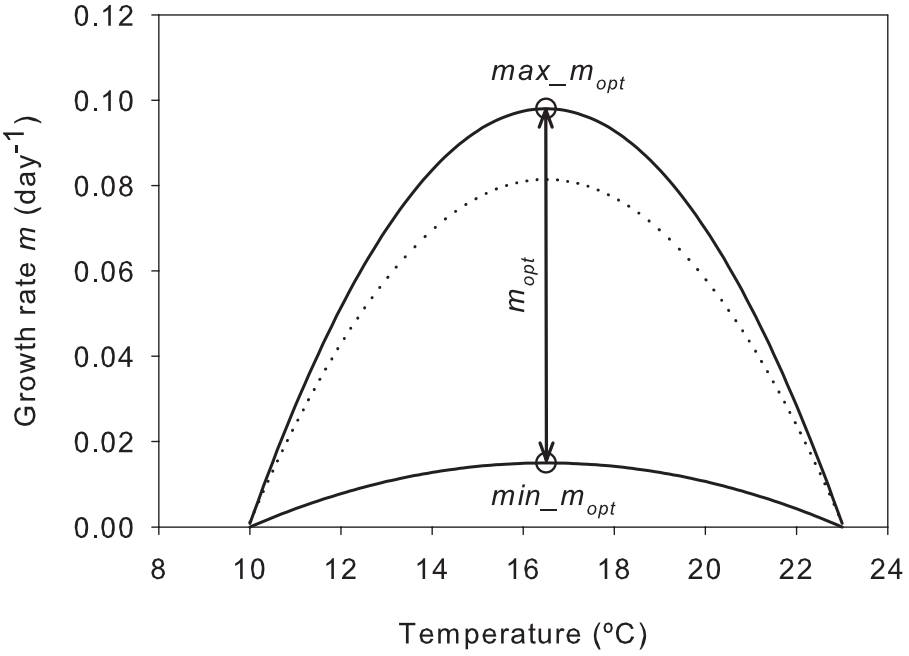


Fig. 4.4 Plot of the exponential growth rate coefficient m as a function of temperature T. Inverted parabolic curves of the form $y = m_{opt} - d(T_{opt} - T)^2$ were used to describe $m(T)$. Inherent growth capacity was represented in the model by randomly selecting an m_{opt} value from a uniform distribution U(min_m_{opt}, max_m_{opt}) and assigning the resulting $m(T)$ curve (e.g. dotted line) to each hatchling at the start of the simulation.

As an initial estimate, the lower limit of the uniform distribution min_m_{opt} was set to 0.0167 (day^{-1}), corresponding to the m_{opt} value observed for *O. pallidus* in the laboratory at 16.5 ºC (André et al. 2009a), and the upper limit max_m_{opt} to 0.098 [day^{-1}], corresponding to highest published growth rate for an octopus species in its exponential growth phase (*Octopus burryi*, Forsythe and Hanlon 1985), so that m_{opt} ~U[0.0167,0.098]. We varied the min_m_{opt} and max_m_{opt} in 0.005 increments, so that min_m_{opt}= and

max_m_{opt}={0.073,0.078,0.083,0.088,0.093}, and tested the resulting uniform distributions looking for a value pair (min_m_{opt}, max_m_{opt}) which reflected the data most accurately in the simulated projection.

Second slower growth phase

In *O. pallidus*, the sub-adult/adult growth phase does not appear to be influenced by temperature and seems to be exponential in form, although slower than the first exponential phase (Hoyle 2002; Semmens et al. 2004). There is, however, no information on the gradient of change in exponential growth between the phases of growth. Therefore, for model parsimony, the second growth phase was represented as linear and tangential to the transition point (t^*, B^*) as employed in Grist and Jackson (2007) (Fig. 4.5).

Sexual maturation

The onset of sexual maturation appears to be dictated by body mass rather than age in the pale octopus, with the mass at 50% maturity estimated for wild females at 472 g (Leporati et al. 2008a). However, the age and body mass at sexual maturity also depends on the food available to an individual (Mangold 1987), although the form of the relationship is not well defined. Given the lack of information on food consumption and its relation to sexual maturity in wild animals, the body mass of the biggest

immature female found in the sampling year from which the data was extracted (i.e. 2005) was asserted to be the maximum body mass achievable by a juvenile in that specific year (i.e. 607g). Therefore, 607g was used as the body mass at which sexual maturity is achieved in the model (Fig.4.5).

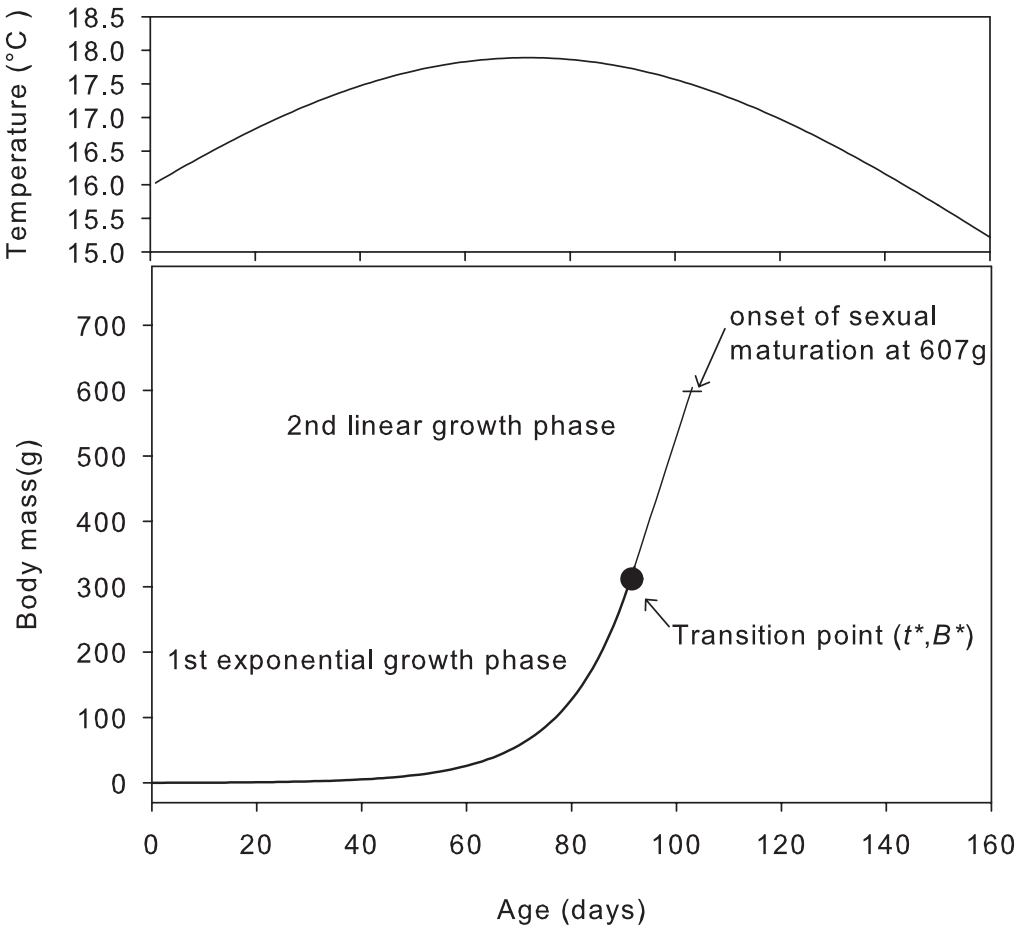


Fig. 4.5 Plot of the projected individual growth trajectory (here a two-phase growth pattern) of a summer-hatched individual parameterised with an initial hatchling size A=0.194 (g), optimum growth rate m_{opt}=0.083 (day^{-1}) and optimum feeding rate f_{opt}=1.49 (kj.day^{-1}).

Other model assumptions

The following model assumptions were also made:

(1) Potential differences in activity levels are not taken into consideration, therefore there is no individual variability in oxygen consumption rate other than that produced by differences in environmental temperature and body mass (i.e. individuals the same size and experiencing the same temperature regime will have identical oxygen consumption rates).

(2) All individuals within a micro-cohort have the same diet (crab) and have access to the same level of food. Hence, there is no individual variability in food consumption other than that produced by differences in environmental temperature and body mass.

(3) As octopus are opportunistic predators, there is no inter-seasonal variation in food consumption (i.e. the feeding parameters remain the same independent of season)

Simulation

Three seasonal micro-cohorts were simulated, each containing 200 individuals, which were started on the 1st day of January (Summer cohort), May (Autumn cohort) and July (Winter cohort) 2005 respectively. Individual juvenile growth trajectories within each micro-cohort were projected until a body mass of 607g, corresponding to the assumed size of maturity. Simulations were aimed at investigating the influence of

environmental temperature, food consumption, hatchling size and inherent growth capacity on size-at-age. Juvenile mortality was not taken into consideration in the projections.

The model was first tuned by adjusting the feeding constant f_{opt}, the feeding exponent p_1 and the range of possible optimum growth rates (min_m_{opt} , max_m_{opt}), until the size-at-age data observed in wild animals were contained within the 5th to 95th percentile range of size-at-age produced by the model for each season.

The influence of seasonal temperature on size-at-age was then investigated for each micro-cohort from projections of the body mass distributions of immature individuals. As the age of the youngest mature animal in each of the seasonal samples varied between 3.75 to 5 months, size-at-age was projected up to 4 months of age (namely at 60, 90 and 120 days) in order to include as many immature simulated individuals as possible in our analyses. The relative influence of individual variability in hatchling size and in inherent growth capacity on simulations was determined independently, by randomising the respective parameters A or m_{opt} whilst holding the other parameter constant either at the mean m_{opt} or mean hatch-size A value (i.e. randomised A with fixed m_{opt} , and randomised m_{opt} with fixed A). The influence of food availability was investigated by altering the f_{opt} value from 0.584 to 2.336 (kj.day^{-1}) in increments of 0.292 (corresponding to 1.5 to 4 times the f_{opt} value estimated

for laboratory animals), and then assessing the impact on size-at-age, the proportion of individuals displaying two-phase growth and age at 50% sexual maturity (estimated here as the age where 50% of individuals have reached 607 g).

RESULTS

The model was fitted by ensuring that the observed data points fell between the 95% bounds (i.e. 5% to 95%) of the model outputs.

Estimation of growth and feeding parameters for wild caught octopus

An m_{opt} range of 0.0217 to 0.0967 (day^{-1}) was necessary to encompass all the variability observed in our sample of wild caught animals and the distribution m_{opt}=U[0.0217,0.0967] was subsequently used for the rest of the analyses. While other feeding parameter combinations provided acceptable model fits under the selected m_{opt} range, the combination of 0.75 (p_1) and 2.044 (f_{opt}) provided the most plausible representation of the predicted size-at-age which tightly surrounded the available data (Fig. 4.6). This combination was used to explore predicted size-at-age at 60, 90 and 120 days, and the age at sexual maturity in our sample.

An f_{opt} value of 0.584 was deemed improbable under natural conditions as it resulted in unrealistically slow growth of individuals. This f_{opt} value was removed from subsequent analyses, so that only the range 0.876 to 2.336 was used to estimate the influence of food intake on size-at-age and age at sexual maturity.

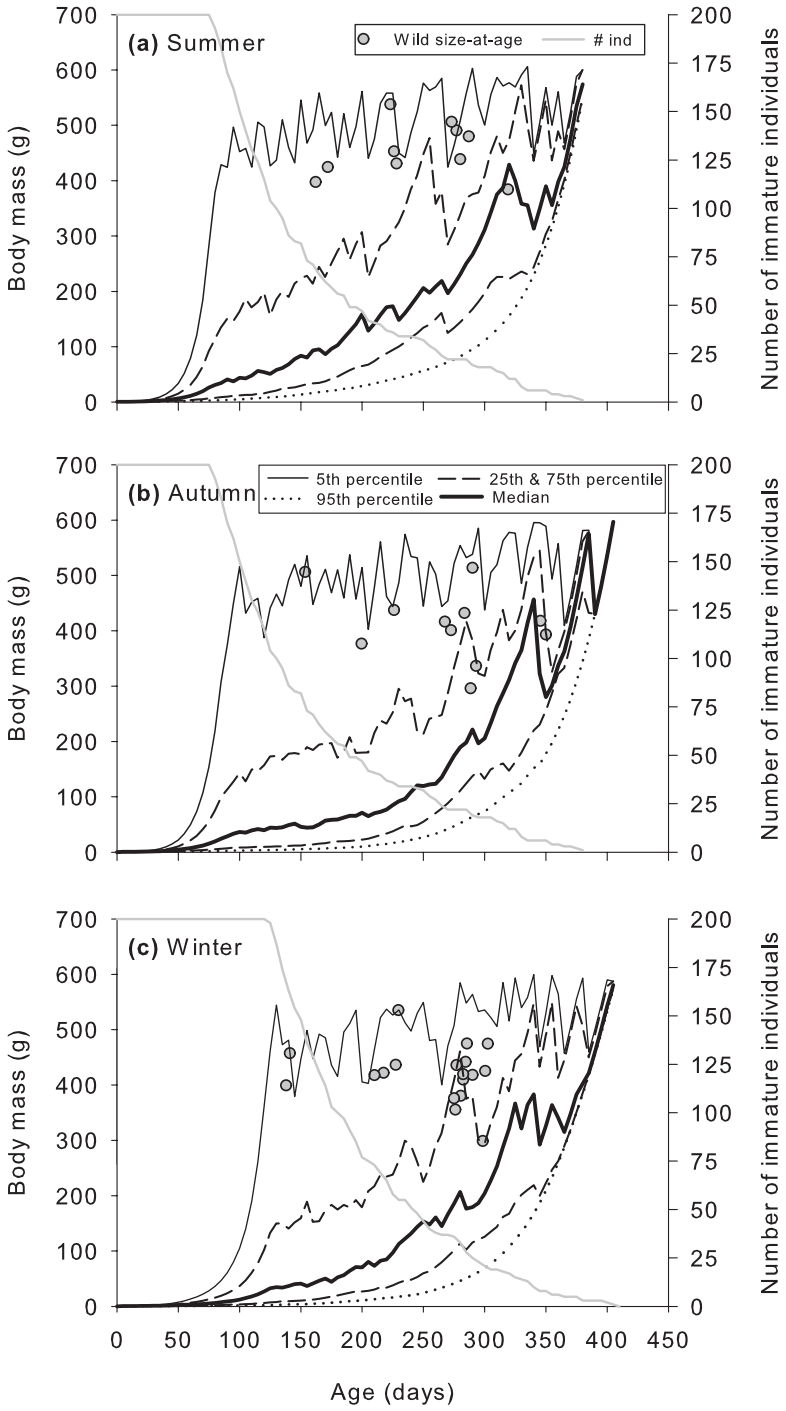


Fig. 4.6 Simulated size-at-age (with both optimum growth rate m_{opt} and hatchling size A randomised) for immature *Octopus pallidus* (n = 200) hatched in a) summer, b) autumn and c) winter. Thin solid lines represent the 5th percentile, dotted lines the 95th percentile, dashed lines the 25th and 75th percentile, thick solid lines the median and solid grey lines the number of immature individuals left in the model. Circles represent the size-at-age data of wild individuals from the Bass Strait fishery.

Projected size-at-age at 60, 90 and 120 days

Size–at-age within a cohort was extremely variable (Fig. 4.7), with up to a 435 fold difference between the smallest and largest individuals at 120 days. Variability increased with time in all seasons but the range of possible sizes attained was smaller for the winter cohort up to 90 days (2.4-579g for summer cohort, 1.4-570 g for autumn cohort and 0.8-119 g for winter cohort). Individuals hatched in summer consistently grew faster and larger than those hatched in other seasons. The autumn cohort was the second fastest growing cohort and presented a similar size-at-age distribution to summer-hatched individuals. At 120 days, 42% of the summer-hatched individuals had reached 607g, against 24.5% of the autumn-hatched individuals, and these individuals were removed from the projection. Winter-hatched individuals presented the smallest size-at-age distribution of the three seasons, reaching only 2/3 of the size of their summer counterparts at 120 days (mean body mass: 83.9 g (n=200) for winter cohort and 126.3 g (n=116) for summer cohort).

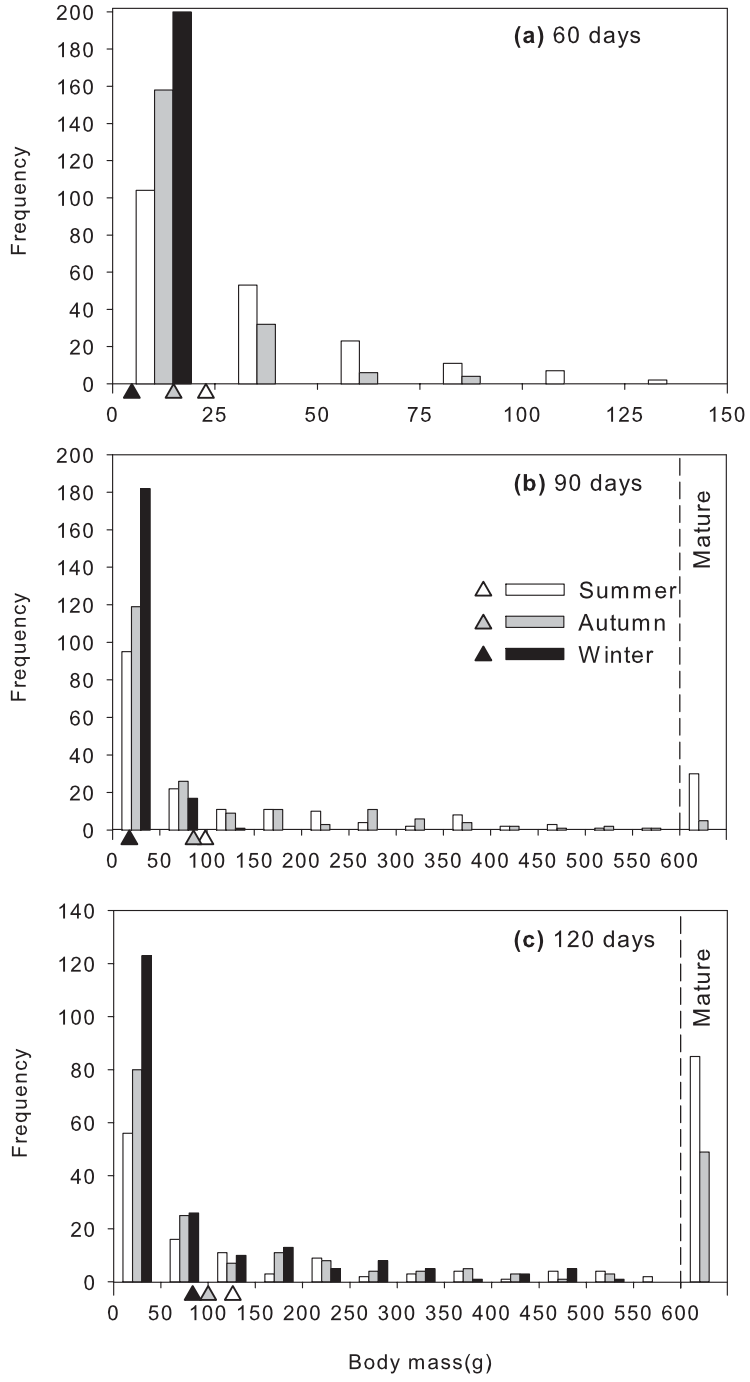


Fig. 4.7 Simulated body mass distributions (with both optimum growth rate m_{opt} and hatchling size A randomised) for summer-, autumn- and winter-hatched *Octopus pallidus* (n = 200) at a) 60, b) 120 and c) 140 days. Seasonal mean body mass are represented with triangles. Note the different x-axis scale for fig. a). Also, note that at 90 and 120 days, some individuals in the summer and autumn simulations had already reached maturity (607 g)

Projected age at sexual maturity

The onset of sexual maturity, represented by a drop in the cohort's median body mass as the first individuals reached 607g and "moved out" of the model, differed between seasons. Summer-hatched individuals reached sexual maturity earlier than individuals hatched in other seasons, with maturation starting at 80 days for the 1st individual and 50% maturation reached at 130 days. Although there was little difference in the age at 50% maturity between autumn and winter-hatched individuals (175 days versus 180 days respectively), maturation started earlier in autumn-hatched individuals, with the 1st individuals starting maturity at 90 days against 125 days for the winter cohort.

Relative influence of hatchling size and inherent growth capacity on size-at-age

Hatchling size produced up to a two-fold difference in size-at-age but generated less variation than inherent growth capacities independent of hatch season (Fig. 4.8). The size-at-age variation observed in our sample of wild-caught animals was not encompassed by either inherent growth capacity or by hatchling size variation alone for the summer cohort.

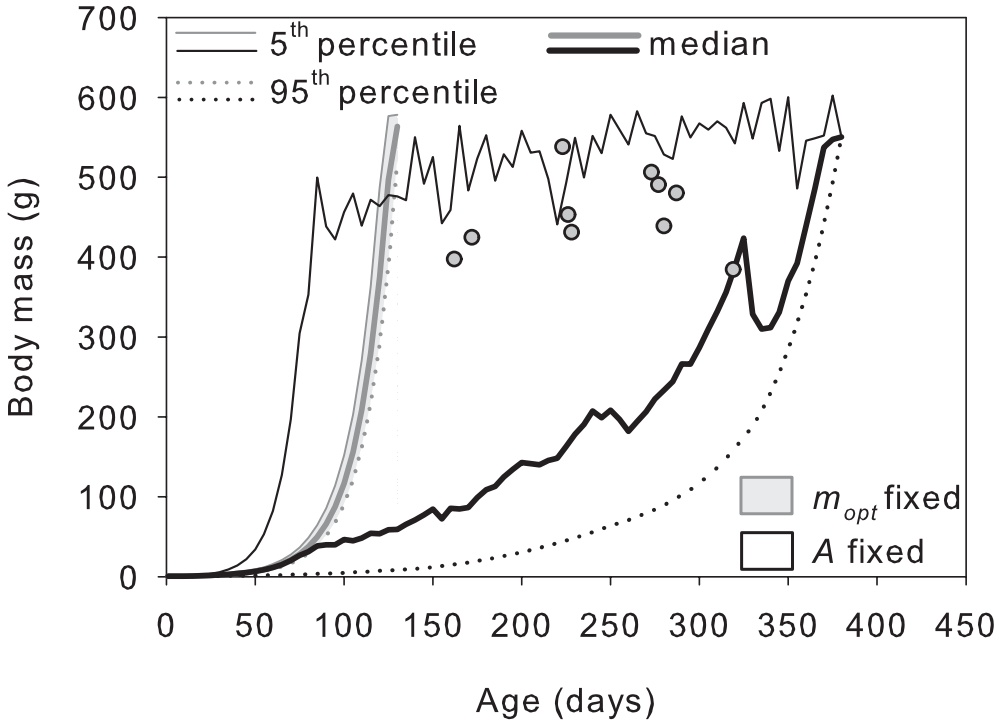


Fig. 4.8 Simulated size-at-age for immature *Octopus pallidus* (n = 200) hatched in summer. The relative influence of individual variability was investigated by fixing hatchling size and randomising growth capacity (A fixed model, black lines), and by fixing inherent growth capacity and randomising hatchling size (m_{opt} fixed model, grey lines). Thin solid lines represent the 5th percentile, dotted lines the 95th percentile, thick solid lines the median and circles the size-at-age data of wild individuals from the Bass Strait fishery. The simulated size-at-age for the autumn and winter cohorts encompassed all the size-at-age data of wild individuals and were not presented here for conciseness.

Projected influence of food intake on size-at-age

The three cohorts presented slightly different patterns with regards to the influence of food availability on size-at-age. For all cohorts, increased food availability resulted in larger individuals, with a range of sizes from 0-350g in summer and 0-100g in autumn and winter for an f_{opt} of 0.876, compared to 0-600g for all seasons for an f_{opt} of 2.336 (Fig. 4.9c, f, i).

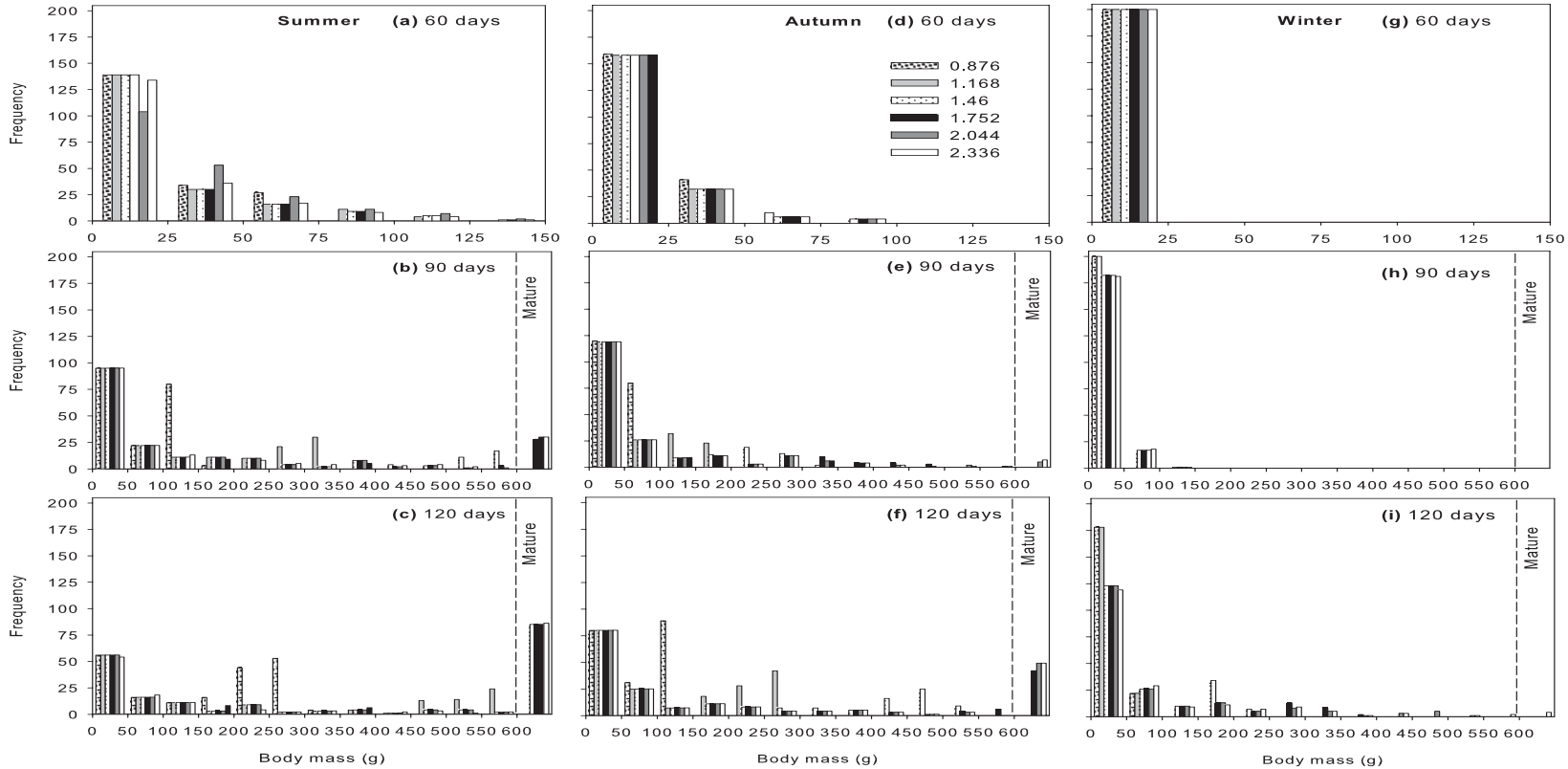


Fig. 4.9 Simulated body mass distributions (with both optimum growth rate m_{opt} and hatchling size A randomised) of 200 summer-hatched (a, b, c), autumn-hatched (d, e, f) and winter-hatched (g, h, i) *Octopus pallidus* at 60, 90 and 120 days under various food availability (f_{opt} =0.876 to 2.336)**.** Note that fig. a), d) and g) are on different scales. Also note that at 90 and 120 days, some individuals in the summer and autumn simulations had already reached maturity (607 g).

The impact of food availability, however, only became apparent at three months of age for the summer and autumn cohorts, and six months of age for the winter cohort, with earlier size-at-age distributions being almost identical and independent of f_{opt}. Summer and autumn cohorts also became bi-modal at 120 days under certain food intake levels, namely f_{opt}=0.876 and 1.168 for summer, and f_{opt}=1.168 and 1.46 for autumn (Fig. 4.9c and f).

Higher food availability also resulted in a lower proportion of individuals displaying two-phase growth within each cohort (Table 4.3). An optimum feeding rate f_{opt} of 2.336 kj.day^{-1} enabled between 87-100% of all individuals to grow exponentially for the entire duration of their juvenile phase depending on the hatching season, whereas f_{opt} values of 0.876 kj.day^{-1} forced between 74.5-89% of all individuals to display two-phase growth.

Table 4.3 Influence of food availability (expressed as f_{opt}) on the percentage of octopus displaying two-phase growth and on the age at which 50% of the cohort reached maturity (50% mat.) for summer-, autumn- and winter-hatched cohorts. A 30 day difference in age at 50% maturity was considered significant.

	Summer		**Autumn**		**Winter**	
f_{opt} **(kj.day^{-1})**	**2-phase (%)**	**Age 50% mat. (days)**	**2-phase (%)**	**Age 50% mat. (days)**	**2-phase (%)**	**Age 50% mat. (days)**
0.876	89	195	79.5	350	74.5	340
1.168	63.5	135	65	210	59	340
1.460	36	130	53	175	45	195
1.752	14	130	39.5	175	30.5	180
2.044	0	130	23.5	175	16.5	180
2.336	0	130	12.5	175	10.5	180

Projected influence of food intake on age at sexual maturity

Increased food availability (up to f_{opt} = 1.46 kj.day^{-1} for the summer and autumn cohorts and f_{opt} = 1.752 kj.day^{-1} for the winter cohort) resulted in earlier sexual maturation, bringing the age at maturity forward by 5 days to 5.8 months. Higher levels of food intake had little or no impact on the age of maturity (Table 4.3, Fig. 4.9c and 4.9f). Summer-hatched individuals consistently matured earlier independent of the feeding rate, reaching maturity between 45 and 205 days before individuals from other cohorts.

DISCUSSION

Food availability has a major impact on size-at-age and age at sexual maturity. Overall, increased food availability results in larger individuals, which is consistent with observations from laboratory experiments on octopus species including *Octopus tetricus* (Joll 1977), *Octopus ocellatus* (Segawa and Nomoto 2002) and *Octopus vulgaris* (Villanueva et al. 2002). The present model suggests that high levels of food intake in the early life-stage delays the switch to a slower growth phase, enabling individuals to grow exponentially for longer periods and reach larger sizes in a shorter time period. While this is evident for the summer and autumn cohorts, the winter cohort appears unaffected by food availability in the first three months post-hatching. Due to their slow growth rates as a response to low water temperatures, individuals from the winter cohort are able to

maintain exponential growth for longer time periods, and only a few experienced a transition in growth phase in the first 90 days post-hatching. Similarly, the apparent lack of influence of food intake on size-at-age in the first two months for the summer and autumn cohorts is linked to the timing of the transition in growth phase. Only very low food intake (e.g. f_{opt}=0.876) enforces a switch in growth rates in the first 60 days post-hatching while other food levels lead to changes at three months of age, or beyond.

High levels of food intake also resulted in earlier sexual maturation in our simulations, which is concordant with previous observations on captive octopus (*Eledone moschata*, Boletzky 1975) and cuttlefish (*Sepia officinalis*, Boletzky 1979). As the onset of sexual maturity is related to size in *O. pallidus* (Leporati et al. 2008a), individuals with high food consumption grow faster and therefore reach the body size at which sexual maturity occurs earlier, independent of the season.

Inherent growth capacity had a strong influence on size-at-age. Growth rates necessary to encompass all the variation in the wild size-at-age sample were substantially higher than growth rates obtained in captivity (Leporati et al. 2007; André et al. 2009a), with an average m_{opt} value for wild animals of 0.0592 against 0.0167 under laboratory conditions (André et al. 2009a). Captivity can alter growth in cephalopods (Joll 1977; Pecl and Moltschaniwskyj 1999) so higher growth rates in wild animals are likely. Alternatively, low growth rates comparable to those obtained in captivity

may be characteristic of some hatchlings from natural populations but these small, slow growing individuals may be unlikely to recruit to the fishery due to size-selective mortality in early life-history (Conover and Schultz 1997; Steer et al. 2003) and gear selectivity of fisheries pots (minimum catch size = 250g). The observation that all the wild size-at-age data (except for one data point in summer), independent of season, were encompassed between the 5th and 50th percentile range of size-at-age produced by the model, is likely a result of the gear selectivity leading to a lack of small specimens (<250g) in our dataset, possibly coupled with low abundance of small animals in the area.

Although secondary to the effect of inherent growth capacity, variations in initial hatchling size still influenced growth. The impact of hatchling size is however likely to be underestimated, as hatchling size distribution used in this study were estimated from one brood only, which possibly under-represented the real range of hatchling sizes in the wild for this species.
Simulation results agreed with the Forsythe Effect, i.e. during the period of decreasing temperatures, individuals grew slower, and earlier hatched cohorts grew larger than subsequent cohorts hatched in cooler conditions. The summer cohort was overall the fastest growing cohort as a result of a combination of larger hatchling size, caused by longer incubation periods over winter and spring, and elevated water temperatures in the first months post-hatching. Autumn and winter hatchling size distributions

were nearly identical due to similar incubation periods, but the autumn cohort benefited from warmer water temperatures, and hence faster growth rates.

There has been extensive debate over the existence of a two-phase growth pattern in wild populations of cephalopods, although this is often observed in captivity (Domain et al. 2000; Jackson and Moltschaniwskyj 2002; Semmens et al. 2004; Arkhipkin 2005; Boyle and Rodhouse 2005). Model simulations suggest that the population comprises a mixture of individuals displaying exponential growth only and two-phase growth, and that the proportion of each depends primarily on individuals' inherent growth capacities and food availability. Low food intake and/or high inherent growth capacity lead to an increase in the proportion of individuals displaying two-phase growth, as animals cannot sustain exponential growth for long periods under these conditions. However, even at the lowest food consumption in the simulations, some individuals never displayed two-phase growth and between 11% (summer cohort) and 25.5% (winter cohort) of individuals in each cohort maintained exponential growth throughout their immature stage. These individuals had low inherent growth capacities, which enabled them to maintain low growth rates despite low food intake. High food consumption ($1.752<f_{opt}<2.336$ kj.day^{-1}) also led to an absence of two phase growth in the summer cohort during the juvenile phase, with all individuals displaying

exponential growth. While being the most "successful", the summer cohort was also the most sensitive to changes in food availability, with proportionally more individuals switching from exponential only to 2-phase growth as f_{opt} decreased. Considering the levels of individual variability in the factors influencing the timing of the transition between the two growth phases, i.e. food consumption, inherent growth capacity, and also variations in metabolic rates due to activity and specific dynamic action (which were not included in this model), it is likely that the fraction of the juvenile population displaying two-phase growth in nature would be variable at any given time. Detecting the existence of a 2-phase growth pattern in a wild population through typical sampling would be very difficult, if not impossible, as growth curves that adequately represent the average behaviour of a population can very poorly describe the pattern followed by any individual in that population (Alford and Jackson 1993). Detection of two-phase growth may be achieved through an intensive mark-recapture program in a natural semi-enclosed area (Van Heukelem 1976). Another possibility would be to explore whether growth increments in stylets correlate with growth rate, in which case two-phase growth could be detected for wild animals.

The impact of maturity on the shape of individual growth curves is unclear. The additional energetic demands associated with reproduction may enforce the shift to a slower growth phase in individuals that have maintained exponential growth during their juvenile phase, and may

impose further reductions in growth rates in individuals that have already shifted out of exponential growth. In any case, the progression of size-at-age distribution in mature individuals is likely to be different from that seen in immature individuals.

This study highlights the importance of coupling size and age data for any population study on cephalopods. Using size data alone to investigate the dynamics of wild populations could be misleading as the size distribution of the summer and autumn cohorts tends to become bimodal with time under certain levels of food availability. While this phenomenon is in effect a consequence of the size difference between individuals that are still in exponential growth versus those that have already switched to a slower growth phase, this bimodality in size distribution could be misinterpreted as being two separate cohorts. This is especially relevant to octopus population studies that have traditionally used Modal Progression Analysis on length-frequency data (Octopus mimus, Cortez et al. 1999; Eledone cirrhosa, Relini et al. 2006) for low-cost fisheries assessment, due to the lack of aging method for these cephalopods. Recent technical developments based on stylet (an internal remnant "shell" unique to octopus) increment analyses now allow aging in octopods (Doubleday et al. 2006; Leporati et al. 2008b) and the current study highlights the importance of accurate age estimates in future population studies.

While encompassing many factors relevant to size-at-age in wild populations, the simulations presented here are still simplistic compared to situations in nature. Larger sample sizes would provide a better estimation of individual variability in the wild and, together with improvements to the metabolic rate term (with inclusion of the energy expended in movement and in post-prandial activity), would produce more precise growth predictions at the individual level. The assumption of constant food consumption independent of seasons may also not be accurate, as food quality and quantity are known to fluctuate seasonally. However, cephalopods are generalists that appear unselective in their choice of prey (Mather 1993; Boyle and Rodhouse 2005), and are therefore likely to find sufficient food all year round, although periods of lower food availability might involve an increase in the energy expended in foraging activities. The simulations nevertheless provide some new insights into growth processes in wild benthic octopus. The shape of the growth curve (and hence size-at-age) is not only strongly influenced by seasonal temperatures during the early post-hatch phase, but also by seasonal temperatures during incubation. While the latter may not be as relevant to species with short incubation periods, such as many squid species or merobenthic octopus species (producing thousands of planktonic hatchlings e.g. *O. vulgaris*), seasonal temperatures during incubation can result in large differences in size at hatching for species

with incubation periods extending over the time frame of a season (e.g. *O. pallidus*).

CONCLUSION

Cephalopod population dynamics are complex due to the short life spans and fast response to environmental conditions of these highly plastic animals. This study has shown the relative influences of the combined, and sometimes counteractive, biotic and abiotic factors on cephalopod growth. Quantifying inherent growth plasticity in octopus is possible and any reasonable attempt to model population dynamics in these species should include in some form or another seasonal temperatures, food availability and individual variations. In the context of predicted warming of the oceans, we can expect some significant changes in the seasonal size-at-age distribution of many octopus species. Shorter incubation periods due to higher water temperatures combined with changes in temperature regimes post-hatching and increased variation in food availability could lead to modifications of the population structure. In the next chapter, models are developed to assess the potential impact of predicted climate change (from a high emission scenario) on the population of pale octopus in Bass Strait.

Ch 5

Predicted effect of climate change on the western Bass Strait pale octopus population

ABSTRACT

Climate change can impact patterns of marine biodiversity through changes in species' distributions and abundance, however, the specific impact of climate change on cephalopod populations is unknown and has never been modelled. In this chapter, the potential response of the Western Bass Strait *Octopus pallidus* population to increased sea temperatures brought about by climate change was investigated. This was achieved by modifying the individual-based bioenergetic model described in the previous chapter and incorporating the resulting outputs into a matrix population model, therefore allowing the inclusion of the effects of individual variability and environment on the vital rates of octopus. Using a climate-change and a no-climate-change scenario, the population was projected from 2005 to 2070 under an array of alternative survivorship schedules and the impact on the population size, population structure, and life history traits were assessed. Projections suggest that increasing water temperatures might not be as beneficial to octopus as previously thought, with the population faring better under the no-climate-change scenario. The population under both climate scenarios was very sensitive to changes in survivorship, with small increases in maximum survivorship resulting in a threefold increase in population size by 2070. Examination of those survivorship schedules that resulted in a balance between population stability and persistence revealed that, after survivorship, egg incubation time was the second most important factor driving the population dynamics of pale octopus under the climate change scenario. While *O. pallidus* has the potential to survive and even prosper under climate change conditions, the population structure and dynamics are likely to change substantially from the present and the no-climate-change scenario, resulting in a potential decrease in average generation time, streamlining of the life cycle and possible loss of resilience to catastrophic events.

INTRODUCTION

It is expected that climate change will alter patterns of marine biodiversity through changes in the distribution and abundance of species. Previous analyses suggest a decline in abundance of many large marine fish species (Hiddink and ter Hofstede 2008), such as North Sea cod (Clark et al. 2003) while populations of other smaller fishes (Hiddink and ter Hofstede 2008) and invertebrates such as jellyfish (Attrill et al. 2007) are predicted to increase. As specified in the General Introduction, the implications of climate change for cephalopods are numerous, but it remains unclear whether these changes will be to the benefit or detriment of octopus populations. Cephalopods may be more strongly and rapidly affected than many longer-lived species by climate change, yet they may also recover more quickly from extreme environmental variations and better adapt to changing conditions (Pierce et al. 2008). Climate change is expected to differentially favour species with wide thermal windows, short generation times and a range of genotypes among its population (Pörtner and Farrell 2008). While octopods have short generation time and some species display wide thermal ranges (e.g. *Octopus ocellatus* with a range of 8°C to 32°C, André et al. 2009), octopus, like most cephalopods, generally lack genetic variation within populations (Doubleday et al. 2009). The high levels of environmentally induced phenotypic variations found in cephalopods (Boyle and von Boletzky 1996) could however compensate for this homogeneity. Advantaged by their lower and less sensitive

metabolism (Zielinski et al. 2001), octopuses will potentially benefit more than squids from climate change, but whether populations will endure under these changing environmental conditions is unknown.

A classical approach to studying population dynamics and investigating the fate of a population under different conditions is to use matrix population models. Matrix population models provide a link between the individual and the population, built around a simple description of the life cycle (Caswell 2001), and have been used widely in ecology from insects (Ma and Bechinski 2008; Schaeffer et al. 2008) to human populations (Zhang and Atkinson 2008). The vital rates (i.e. birth, growth, maturation, fecundity and mortality rates) describe the transition of individuals through the life-cycle and determine the subsequent dynamics of the population. Applying matrix population models to cephalopods is challenging because the in-depth understanding of the life-cycle and of the variation in (highly individually plastic) vital rates essential for this type of analysis, is lacking for most species. To date, only Katsanevakis and Verriopoulos (2006) have attempted to use a matrix modelling approach to investigate cephalopod population dynamics. In their study, the authors developed a size-structured matrix population model to investigate the transient seasonal population dynamics of *Octopus vulgaris* in eastern Mediterranean waters. Their matrix population model was incomplete, however, due to a lack of data on fecundity, and on egg and paralarval

densities (Katsanevakis and Verriopoulos 2006). Estimation of these parameters is essential for the complete life-cycle to be investigated.

Outputs from bioenergetic models have been used successfully to estimate the parameters of matrix population models (Liao et al. 2006; Neer et al. 2007) when data are too expensive or complicated to obtain through traditional methods. Bioenergetic models are useful as they provide a link between the animal's physiology and environmental conditions, and coupling individual-based bioenergetic models and matrix population models is a powerful approach for relating the population level to changes in environmental conditions that affect growth, mortality and reproduction (Neer et al. 2007).

The aim of this chapter was to investigate the potential response of the female component of the western Bass Strait *Octopus pallidus* population to increased sea temperatures brought about by climate change. This was achieved by modifying the individual-based bioenergetic model described in the previous chapter and incorporating the resulting outputs into a complete matrix population model. This approach allowed the inclusion of the effects of individual variability and environment on the vital rates of octopus, which was essential given the importance of these factors in the life history of octopods, as highlighted throughout this thesis. Using a climate-change (CC) and a no-climate-change (noCC) scenario, the

population was projected from 2005 to 2070 under various survivorship schedules and the impact on the population size and structure was assessed. Both the CC and noCC climate scenarios were based on sea surface temperature (SST) predictions for the Bass Strait region. The year 2005 was selected as the year to initiate the simulations, and as the year of reference for the noCC scenario, because the majority of available age, reproductive and morphometric data for wild *O. pallidus* were collected in that specific year.

METHODS

General form of the model

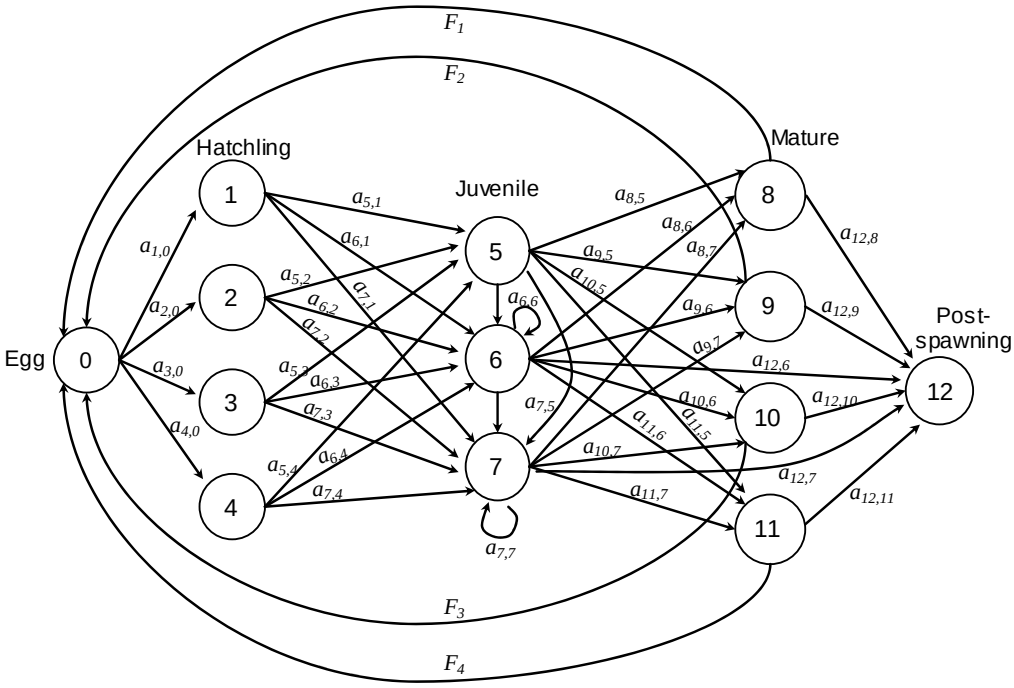
The model used in this chapter is a stage-based model (Caswell 2001), which was chosen since many of the parameters in pale octopus are size specific rather than age specific. The final model structure contained thirteen stages, with twelve size classes, ranging from egg to post-spawning animals, and a final "plus-group" or "absorbing" stage. Stage E represents the egg class, J1, J2, J3 and J4 represent the hatchling classes, J5, J6 and J7 the juvenile classes, M1, M2, M3 and M4 the reproductively mature classes (not to be confused with denomination for stages of maturity), and PS the post-spawning class (i.e. absorbing stage). Pale octopus are terminal spawners and animals entering the post-spawning class do not contribute further to the population, and are removed from the model (i.e. have zero survivorship). Due to the large individual

variability in size at maturity present in octopus, the size class for the last juvenile stage (J7) overlaps with the size classes for the first two mature stages (M1 and M2). A diagram of the life cycle and the size classes chosen for the various stages are presented in Fig. 5.1.

The model is of the form

$$N(t+1) = P(t) \times S \times N(t) \qquad (25)$$

where $N(t)$ is a (13x1) vector representing the number of individuals in each stage at time t, S is a (13x13) square matrix whose diagonal represents the probability of survival in each stage (i.e. the survival matrix) and $P(t)$ is the (13x13) population projection matrix at time t, which provides the probabilities $a_{j,i}$ of the octopus moving from stage i to stage j during the projection interval, as well as the fecundity F of each mature stage (Fig.5.2). The projection interval (from t to t+1) is three months, enabling a seasonal analysis of the population dynamics.



Stage #	0	1	2	3	4	5	6	7	8	9	10	11	12
Stage	egg	J1	J2	J3	J4	J5	J6	J7	M1	M2	M3	M4	PS
Size class (g)		0-0.125	0.125-0.25	0.25-0.375	0.375-0.5	0.5-10	10-100	100-700	200-450	450-700	700-950	950-1200	

Fig. 5.1 Diagram of the life cycle of *Octopus pallidus*, showing the various stages and the corresponding size classes. Probabilities $a_{j,i}$ correspond to the probabilities of an octopus moving from stage i to stage j during the projection interval and F represent the fecundity of each mature stage.

$$P = \begin{pmatrix} a_{0,0} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & F1 & F2 & F3 & F4 & 0 \\ a_{1,0} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ a_{2,0} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ a_{3,0} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ a_{4,0} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ a_{5,0} & a_{5,1} & a_{5,2} & a_{5,3} & a_{5,4} & a_{5,5} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ a_{6,0} & a_{6,1} & a_{6,2} & a_{6,3} & a_{6,4} & a_{6,5} & a_{6,6} & 0 & 0 & 0 & 0 & 0 & 0 \\ a_{7,0} & a_{7,1} & a_{7,2} & a_{7,3} & a_{7,4} & a_{7,5} & a_{7,6} & a_{7,7} & 0 & 0 & 0 & 0 & 0 \\ a_{8,0} & a_{8,1} & a_{8,2} & a_{8,3} & a_{8,4} & a_{8,5} & a_{8,6} & a_{8,7} & 0 & 0 & 0 & 0 & 0 \\ a_{9,0} & a_{9,1} & a_{9,2} & a_{9,3} & a_{9,4} & a_{9,5} & a_{9,6} & a_{9,7} & a_{9,8} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & a_{10,5} & a_{10,6} & a_{10,7} & a_{10,8} & a_{10,9} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & a_{11,5} & a_{11,6} & a_{11,7} & a_{11,8} & a_{11,9} & a_{11,10} & 0 & 0 \\ 0 & 0 & a_{12,2} & a_{12,3} & a_{12,4} & a_{12,5} & a_{12,6} & a_{12,7} & a_{12,8} & a_{12,9} & a_{12,10} & a_{12,11} & 0 \end{pmatrix}$$

Fig. 5.2 Population projection matrix *P* for *Octopus pallidus*, based on the life cycle diagram in Fig. 5.1. All post-hatch transition probabilities $a_{j,I}$ (in light grey) were determined using the bioenergetics model, while egg to hatchling transition probabilities (in dark grey) were calculated using the projected incubation times. Fecundities *F* (in black) were determined using reproductive data from wild octopus in Bass Strait.

Bioenergetics model

The predictions of the bioenergetic model developed in Ch. 4 (André et al. 2009b) were used to estimate the post-hatch transition probabilities $a_{j,i.}$ of the population projection matrix *P*(t) (Fig 5.2).

The Dynamic Temperature-dependent Energy Balance Model (DTEBM) was extended to include mature stages to permit the prediction of the growth of individual females within cohorts, from hatching through to egg-laying, under a warming water temperature scenario (i.e. climate change) which was compared with a stable water temperature scenario (i.e.

no climate change). To provide estimates of the vital rates needed to generate the population projection matrices under different temperature conditions, simulations were run for individuals hatched in 2005, 2030, 2050 and 2070. Individual variability was added at 3 levels: hatchling size (A), inherent growth capacity (m_{opt}) and body mass at maturity (B_{mat}). Body mass for each individual was updated daily until individuals reached their egg-laying body mass.

Water temperature

Two daily temperature functions were developed, representing the climate-change (CC) and the no-climate-change (noCC) scenarios. Both functions were based on a 360 day year (30 days per calendar month), starting on the 1st January 2005 and ending on 31st December 2070.

The CC scenario temperature function was based on a high emission scenario (A1FI) of the IPCC (IPCC 2000). This specific scenario was selected because recent studies have shown that current temperatures and carbon dioxide emissions are already on the upper limit of the climate predictions (Rahmstorf et al. 2007). Predictions of temperature in 2070 for the western Bass Strait region (Fig. 5.3) under the A1FI scenario were provided by CSIRO (Alistair Hobday, Climate Adaptation Flagship). Predictions were obtained by downscaling data (Fig. 5.3) from a suite of nine Global Climate Models and accessed using the CSIRO tool "OzClim for Oceans". A linear increase in the mean annual temperature between

the 2005 and 2070 was assumed (Fig 5.4a) and the resulting temperature function was of the form

$$T = T_0 + T_1 \cos k\left(t + t_{hatch} + c\right) \text{ where } T_0 = T_{0_1}\left(t + t_{hatch}\right) + T_{0_2} \quad (26)$$

and where T_0 is the mean annual temperature (baseline), T_{0_1} and T_{0_2} are constants, T_1 is the annual fluctuation of temperature around T_0 (amplitude), k is the frequency, c is the time lag necessary to align the maximum of the curve to the occurrence of the maximum temperature in a year (shift), t_{hatch} is the hatching day in a 360 day year and t is the age of the individual (in days). The CC scenario implied that the predicted maximum temperature in 2005 was 17.32°C while it was 19.43°C in 2070, a difference of 2.11°C.

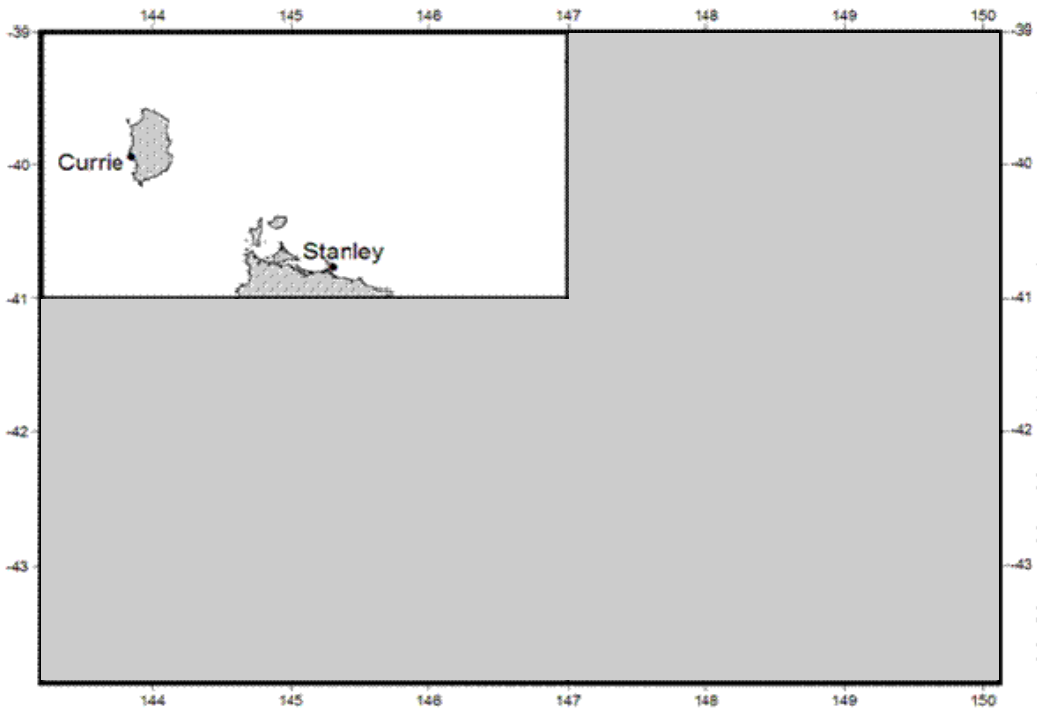


Fig. 5.3 Map showing the western Bass Strait sector to which the downscaling of the sea surface temperature (SST) predictions in 2070 under the A1FI climate change scenario was applied. Data provided by CSIRO (Alistair Hobday, Climate Adaptation Flagship).

The noCC scenario temperature function was based on the assumption that temperature does not increase in the Bass Strait region and is identical to the temperature regime experienced in 2005 (Fig 5.4b).

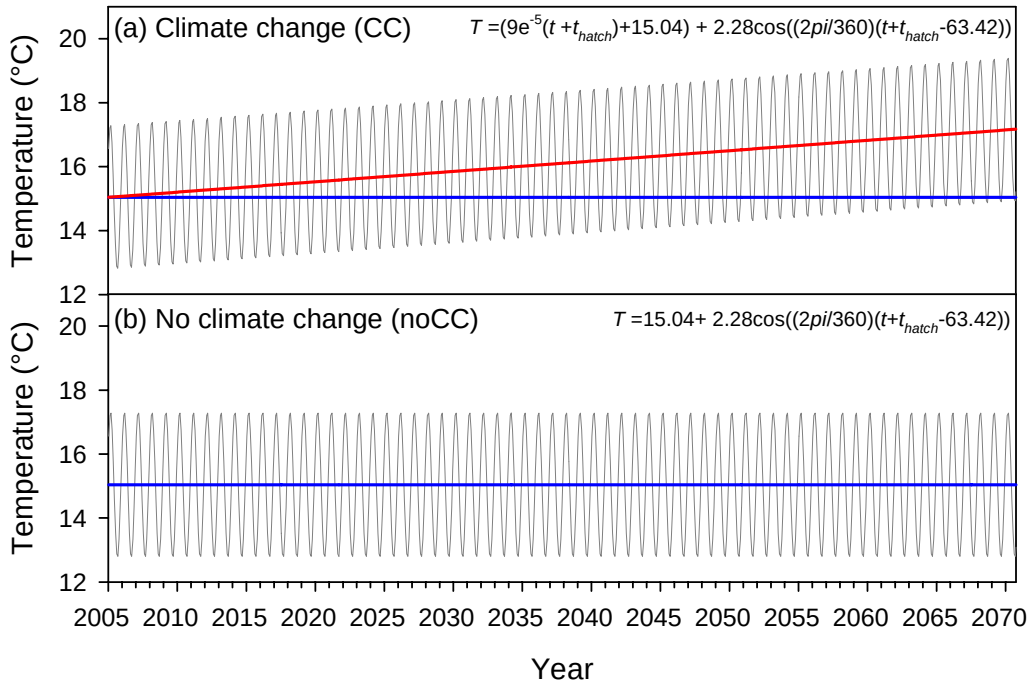


Fig. 5.4 Temperature functions used in the bioenergetic model for a) the climate change scenario (CC) and b) the no climate change scenario (noCC). The blue line represents the mean temperature during the noCC scenario, the red line the mean temperature during the CC scenario.

Hatchling size

Hatching was set on the 1st of January (summer cohort), 1st April (autumn cohort), 1st July (winter cohort) and 1st October (spring cohort). Hatchling

size distribution was dependent on temperature and incubation duration (see Fig. 4.3, page 100), as per the relationships defined in Ch. 4. A narrowing of each seasonal hatchling size distribution and a decrease in mean hatchling size were predicted with time under the CC scenario. The predicted seasonal hatching size distributions for the years 2005, 2030, 2050 and 2070 are presented in Fig 5.5. For the noCC scenario, only the seasonal hatchling size distributions for 2005 were used.

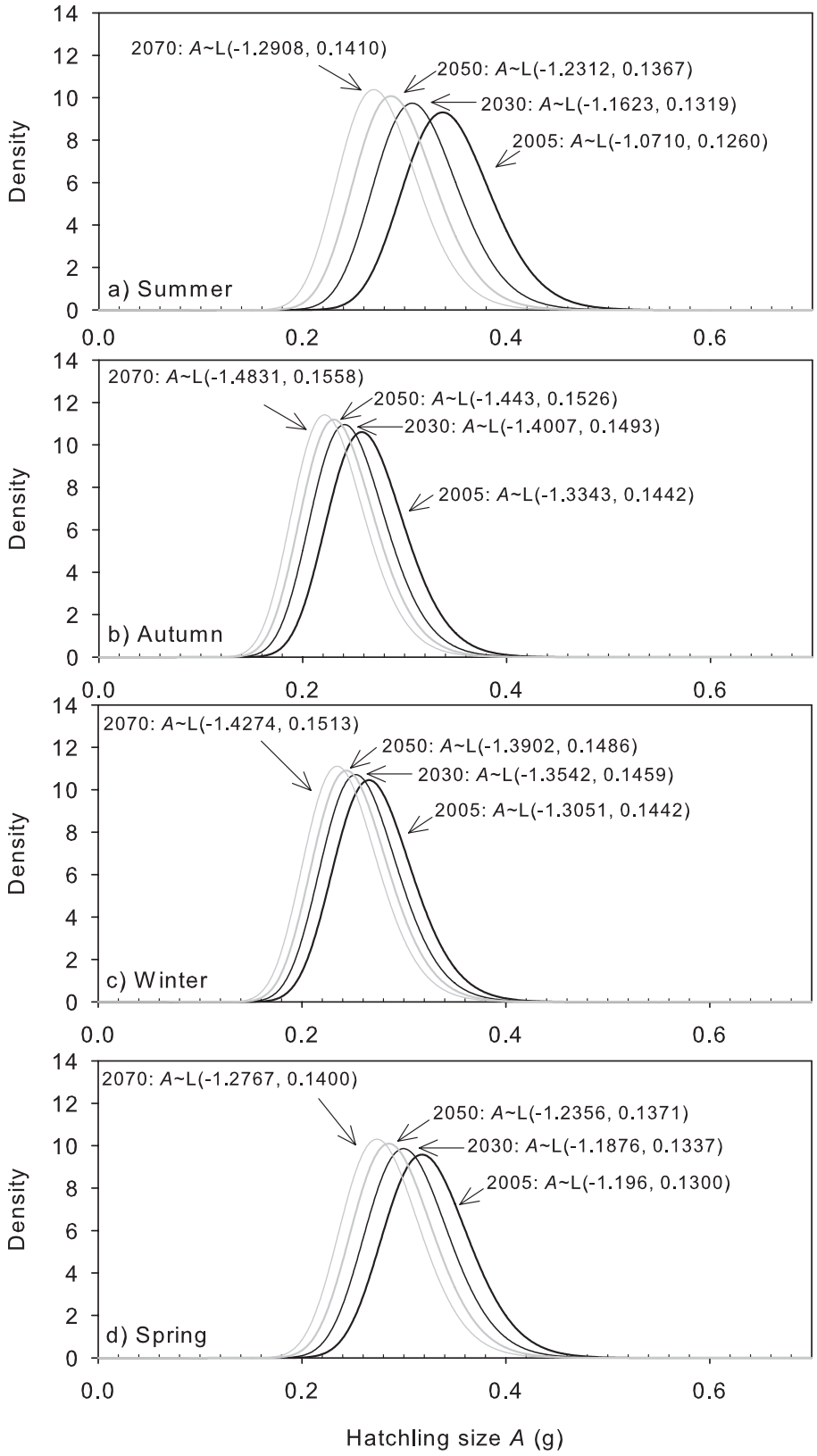


Fig. 5.5 Predicted seasonal hatchling size distributions in 2005, 2030, 2050 and 2070 in a) summer, b) autumn, c) winter and d) spring. Hatchling size was described by a lognormal distribution $A \sim \mathrm{L}(\mu, \sigma)$ where $\mu = \ln(m)$ and m is the median of the distribution.

Inherent growth rate and sexual maturity

As specified in Ch.4, the onset of sexual maturation in the pale octopus appears to be largely driven by body weight, which is related to growth rate. Inherent growth capacity (m_{opt}) and body weight at sexual maturity (B_{mat}) were therefore treated as co-variates and selected, for each individual, from a bivariate normal distribution:

$$\left(B_{mat}, m_{opt}\right) \sim N\left(\mu_{B_{mat}}, \mu_{m_{opt}}, \sigma^2_{B_{mat}}, \sigma^2_{m_{opt}}, \rho_{B_{mat} m_{opt}}\right) \quad (27)$$

It was assumed that:

(1) B_{mat} was temperature dependent, based on the general observation that high temperatures lead to reproduction at small sizes (Mangold 1987).

(2) The relationship between temperature (T) and the mean $\mu_{B_{mat}}$ of the B_{mat} distribution was negatively linear. Based on a difference of 10g in mean body mass at maturity between 2005 (mean B_{mat}=466g) and 2006 (mean B_{mat}=456g) samples (Leporati, pers. comm.) and a difference in mean annual temperature T_0 of 0.3°C between two years, the change in $\mu_{B_{mat}}$ was estimated at -33.3g per 1°C increase in temperature. Assuming, from the temperature projection, a yearly increase in mean annual water temperature of 0.0324°C over the next 65 years, the value of $\mu_{B_{mat}}$ as a function of time can be expressed as $\mu_{B_{mat}}(year) = -1.07892\,year + 2629.235$ (fig 5.6)

(3) The variance of the B_{mat} distribution was assumed constant.

(4) Inherent growth capacity m_{opt} was by nature temperature independent and ranged from 0.0217 and 0.0967, as estimated in Ch. 4.

(5) Individuals with higher m_{opt} reached sexual maturity at a smaller body mass

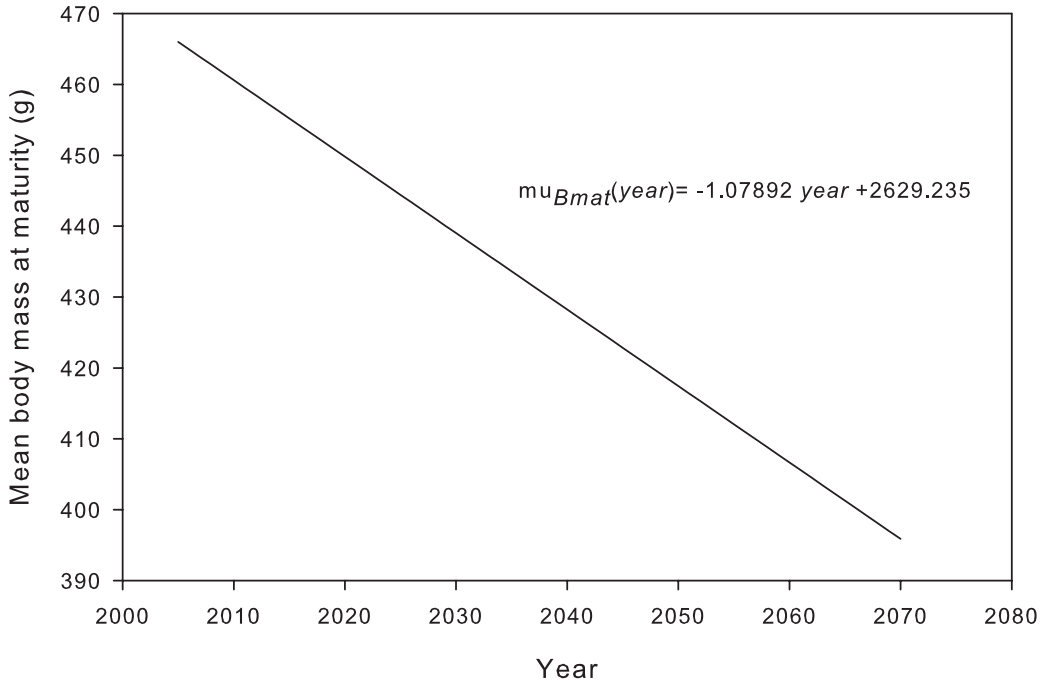


Fig. 5.6 Estimated mean body mass at maturity $\left(\mu_{B_{mat}}\right)$ used to calculate the bivariate normal distribution $\left(B_{mat}, m_{opt}\right) \sim N\left(\mu_{B_{mat}}, \mu_{m_{opt}}, \sigma^2_{B_{mat}}, \sigma^2_{m_{opt}}, \rho_{B_{mat}m_{opt}}\right)$.

The resulting bivariate normal distributions can be expressed as: $\left(B_{mat}, m_{opt}\right) \sim N\left(\mu_{B_{mat}}(year), 0.0592, 4900, 0.00012, -0.7\right)$, which are illustrated for the years 2005, 2030, 2050 and 2070 in Fig 5.7. For the noCC scenario, only the bivariate normal distribution for 2005 was used.

Body mass at egg-laying

Based on the observation that mature males are present all year round in Bass Strait (Leporati et al. 2008a) and that female octopus may copulate before maturity and store sperm (Mangold 1987; Rodríguez-Rúa et al. 2005), it was assumed that egg-laying occurred within a week of individuals reaching sexual maturity. Body mass at egg deposition was therefore calculated by extending the growth trajectory (exponential or linear) that individuals were following at the time of sexual maturity for a further seven days. In cases where the switch in growth phase occurred during these seven days, the growth trajectory was changed to reflect the slowing growth rate.

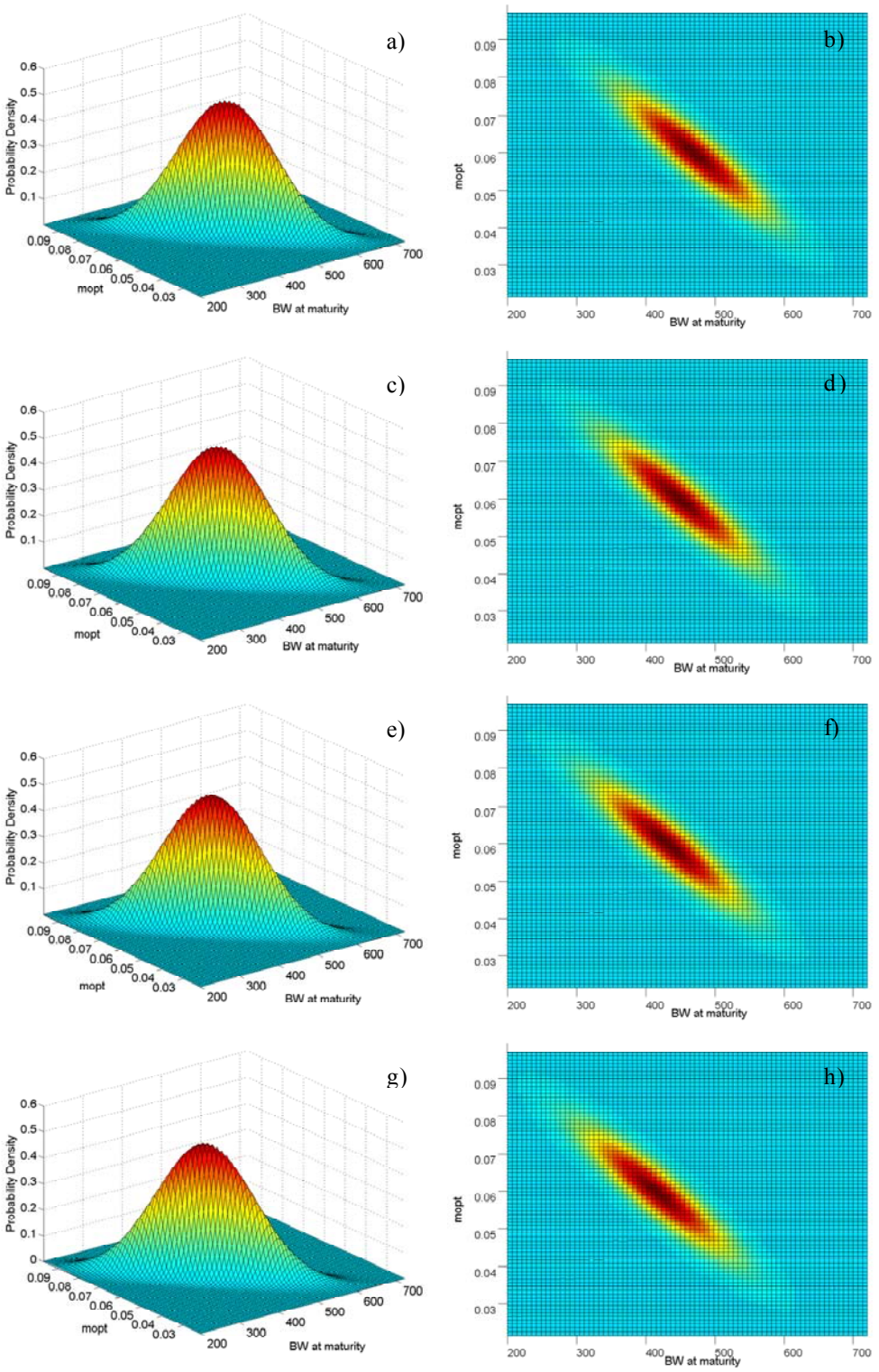


Fig. 5.7 3-D and 2-D representations of the bivariate normal distributions of Inherent growth capacity (m_{opt}) and body weight at sexual maturity (B_{mat}) for the years a) and b) 2005, c) and d) 2030, e) and f) 2050, and g) and h) 2070.

Simulations

Simulations were run for each season (starting on the 1st of January, April, July and October) for the years 2005, 2030, 2050 and 2070. One hundred micro-cohorts were generated by season, each containing 400 females. Mortality was not included in the simulations and individual growth trajectories within seasonal micro-cohorts were projected until individuals reached egg-laying. For each individual, hatchling size (A) was selected randomly from the corresponding hatchling size distribution (fig 5.5) while inherent growth capacity (m_{opt}) and body weight at sexual maturity (B_{mat}) were selected randomly from the corresponding bivariate normal distribution (fig 5.7). Other feeding, metabolic and growth parameters for the model were identical to that used in Ch. 4; the parameter values for the bioenergetics model are summarised in Table 5.1.

Table 5.1 Equations and parameter values for the modified dynamic temperature-dependent energy balance model (DTEBM). *A* is the hatchling size, *t* is the age (in days) and t_{hatch} the hatching day in a 360 day year.

Eq	Equations and parameters	Values	
(13)	**Growth rate *G*:** $q_3 B$ **with** $q_3 = k_3\left(m_{opt} - d\left(T_{opt} - T\right)^2\right)$		
	Optimum temperature for growth (T_{opt}) (°C)	16.5	
	Growth rate coefficient at T_{opt} (m_{opt}) (day^{-1})	from bivariate distribution (Eq.27)	
	Energy equivalent of octopus tissue (k_3) (kj.g^{-1})	4.05848	
(15)	**Feeding rate *F*:** $q_1 B^{p_1}$ with $q_1 = f_{opt} - d_f\left(T_{fopt} - T\right)^2$		
	Optimum temperature for feeding (T_{fopt}) (°C)	18.4	
	Feeding rate at T_{fopt} (f_{opt}) (kj.day^{-1})	2.044	
	Parabolic constant (d_f) if $T \leq T_{fopt}$	0.029	
	$T > T_{fopt}$	0.0966	
	Feeding rate exponent (p_1)	0.75	
(16)	**Metabolic rate *M*:** $q_2 B^{p_2}$ **with** $q_2 = k_1 e^{\left(a_2 + \frac{b_2}{T + k_2}\right)}$		
	Metabolic rate exponent (p_2)	0.88	
	Conversion factor O_2 mg.h^{-1} to kj. day^{-1} (k_1)	0.33758	
	Conversion factor °K to °C (k_2)	273.15	
	Constant (a_2)	21.80	
	Constant (b_2)	-6952.8	
(18)	**Temperature *T*:** $T_0 + T_1 \cos\left(k\left(t + t_{hatch} + c\right)\right)$	**Climate change**	**No change**
	Baseline (T_0)	$9e^{-5}$ $(t+t_{hatch})$+15.04	15.04
	Amplitude (T_1)	2.28	2.28
	Frequency (k)	$2\pi/360$	$2\pi/360$
	Shift (c)	-63.42	-63.42
(20)	**Body mass *B*:** $Ae^{\int_0^t m(t)}$		
(27)	**Body mass at maturity (B_{mat}), and (m_{opt})**	$\left(B_{mat}, m_{opt}\right) \sim N\left(\mu_{B_{mat}}(year), 0.0592, 4900, 0.00012, -0.7\right)$	
		with $\mu_{B_{mat}}(year) = -1.07892\,year + 2629.235$	

Post-Hatchling Transition probabilities $a_{j,i}$

The bioenergetic model was run and the predicted number of individuals in each size-class (J1 to PS) were summarized at three month intervals, until all 400 individuals in the simulation had entered the PS size class. The probabilities of individuals moving from one class to another (the $a_{j,i}$) in the space of a three monthly season were then computed, resulting in four seasonal transition probability matrices per simulated year (i.e. 2005, 2030, 2050 and 2070). Seasonal transition probabilities matrices for the years between these selected years were obtained by linear interpolation between each seasonal matrix (Fig. 5.8).

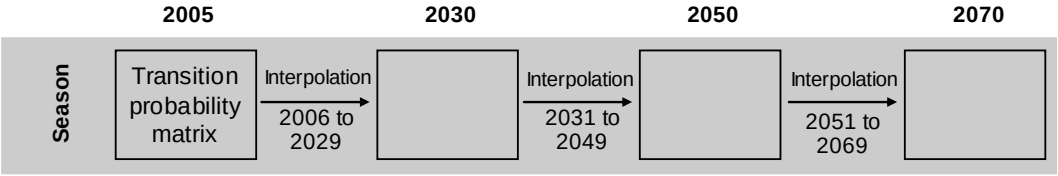


Fig. 5.8 Diagram representing the method for estimating yearly seasonal transition probabilities matrices from the 2005, 2030, 2050 and 2070 seasonal transition probabilities matrices. The interpolation is a simple linear change between the estimated proportions.

Matrix population model

Projection matrix P(t)

A total of 264 projection matrices were used for the CC scenario (four seasonal projection matrices per year between 2005 and 2070, Table 5.2) while only four projection matrices were used for the noCC scenario (corresponding to the four seasonal matrices of the year 2005, Table 5.3).

Table 5.2 Sequence of modelling under the climate change scenario (CC). *P* corresponds to one of 264 projection matrices, *S* the survival matrix and *N*(*t*) the population at time *t*.

Season	Time (*t*)	Population *N*(*t*)
Summer 2004/05	0	$N(0)$
Autumn 2005	1	$N(1)=P(autumn\ 05) \times S \times N(0)$
Winter 2005	2	$N(2)=P(winter\ 05) \times S \times N(1)$
Spring 2005	3	$N(3)=P(spring\ 05) \times S \times N(2)$
Summer 2005/06	4	$N(4)=P(summer\ 05) \times S \times N(3)$
Autumn 2006	5	$N(5)=P(autumn\ 06) \times S \times N(4)$
⋮	⋮	⋮
Summer 2069/70	261	$N(261)=P(summer\ 69) \times S \times N(260)$
Autumn 2070	262	$N(262)=P(autumn\ 70) \times S \times N(261)$
Winter 2070	263	$N(263)=P(winter\ 70) \times S \times N(262)$
Spring 2070	264	$N(264)=P(spring\ 70) \times S \times N(263)$

Table 5.3 Sequence of modelling under the no climate change scenario (noCC). *P* corresponds to one of four projection matrices, *S* the survival matrix and *N*(*t*) the population at time *t*.

Season	Time (*t*)	Population *N*(*t*)
Summer 2004/05	0	$N(0)$
Autumn 2005	1	$N(1)=P(autumn\ 05) \times S \times N(0)$
Winter 2005	2	$N(2)=P(winter\ 05) \times S \times N(1)$
Spring 2005	3	$N(3)=P(spring\ 05) \times S \times N(2)$
Summer 2005/06	4	$N(4)=P(summer\ 05) \times S \times N(3)$
Autumn 2006	5	$N(5)=P(autumn\ 05) \times S \times N(4)$
⋮	⋮	⋮
Summer 2069/70	261	$N(261)=P(summer\ 05) \times S \times N(260)$
Autumn 2070	262	$N(262)=P(autumn\ 05) \times S \times N(261)$
Winter 2070	263	$N(263)=P(winter\ 05) \times S \times N(262)$
Spring 2070	264	$N(264)=P(spring\ 05) \times S \times N(263)$

Egg to Hatchling Transition probabilities $a_{j,i}$

Transition probabilities for the post-hatch stages were obtained from the outputs of the bioenergetics model, as described above, however, the transition probabilities between the egg and hatchling stages were derived from a consideration of the relationship between the environmental temperature and incubation time (see eq. 24 in Ch. 4 p. 98). With time steps of three months and incubation sometimes exceeding 6 months, the timing of the transitions for different seasons have the potential to overlap, complicating the estimation of the transition probabilities.

Fecundities F

The fecundities for each of the mature size classes (M1 to M4) were derived from data from Leporati et al. (2008a). The relationship between female body weight (g) and number of eggs was determined by a model II regression, based on 155 mature females taken from the Bass Strait region between 2004 and 2006 (Fig. 5.9). The fecundity for a stage was assumed to be the fecundity at the mean body weight for that stage (Fig. 5.9) and was also assumed to remain constant independent of the projection year. Fecundity was estimated at 325 eggs for stage M1, 637 eggs for stage M2, 950 eggs for stage M3 and 1262 eggs for stage M4. As the present model represents the dynamics of females, only those eggs that produced females were taken into account. There is no information on sex ratio at hatching for octopus but work on cuttlefish (Montalenti and Vitagliano 1946)

suggest a 1:1 male:female sex ratio. The stage-specific fecundities were therefore divided by two.

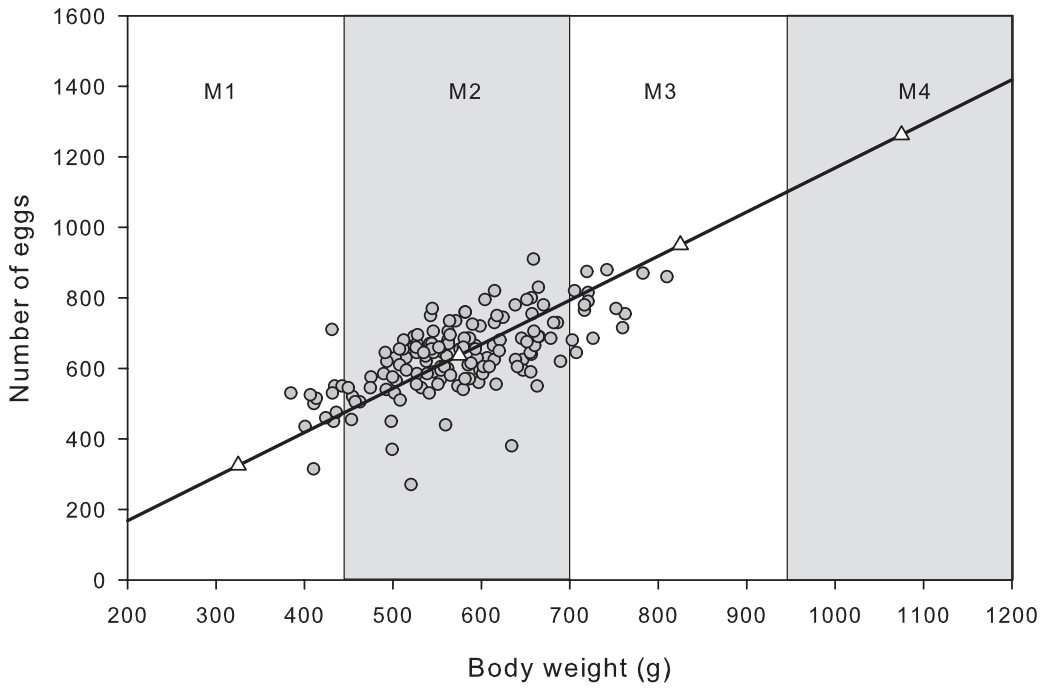


Fig. 5.9 Estimated relationship between body mass in mature females and number of eggs using a type II regression. Circles represent data on 155 wild mature females from the Bass Strait region, taken between 2004 and 2006. White triangles represent the mean body weight for the mature stage. Data courtesy of Stephen Leporati.

Survival matrix S

For the purpose of the model, egg survival and post-hatch survival were treated separately.

Egg survival

Various factors influence egg survival in cephalopods, including environmental temperature (Gowland et al. 2002a; Gowland et al. 2002b),

predation, biofouling (Steer and Moltschaniwskyj 2007) and water salinity (Paulij et al. 1990; Sen 2005). As female octopus brood their eggs, mortality from predation and biofouling were considered to be insignificant. Following the approach of Cinti et al.(2004), a temperature-dependent egg survival curve was developed, scaling the survival curve of *Loligo gahi* to the known thermal range of *O. pallidus* (i.e. 10°C to 23°C, Stranks 1996) (Fig 5.10). Mean incubation temperatures remained within the optimal range in the simulations so that temperature was assumed to have no effect on egg survival in the model. Egg survival was therefore considered a fixed value for the purpose of the simulations and was set to 75% corresponding to the average hatching success of *Eledone moschata* (Mangold 1983a), a species with a similar life-cycle to *O. pallidus*.

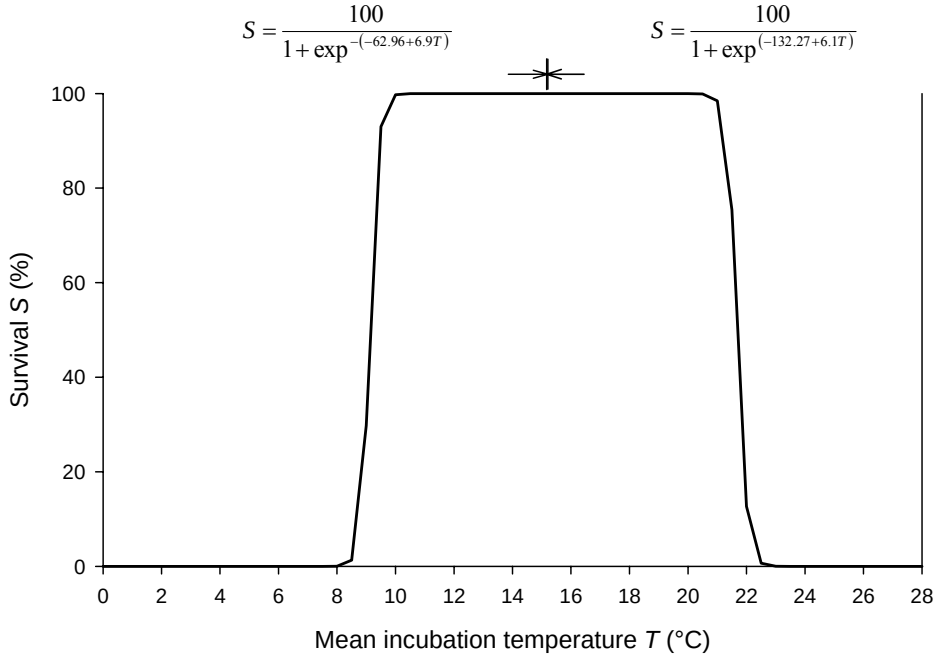


Fig. 5.10 Relationship between mean incubation temperature and egg survival for *O. pallidus* (adapted from the egg survival curve of *Loligo gahi* by Cinti et al. (2004)).

Post-hatch survival

Survival in the wild is difficult to estimate for marine species and there are no data on survival of octopus in their natural habitat. Modelling natural mortality with age in cephalopods has been attempted by Caddy (Caddy 1996) but these estimations could not be adapted to the present matrix population model, which is stage based. Based on the general observation that smaller individuals incur higher mortality (Conover and Schultz 1997; Steer et al. 2003), post-hatch survival was assumed to be size-dependent and was represented by a logistic model with the lowest survivorship being exhibited by the smallest size class (J1). In the absence of information concerning survival in the wild the implications of thirty alternative logistic curves were investigated in order to bracket the possible outcomes from different regimes of survivorship. In each case the logistic curve was defined by a combination of minimum survivorship in J1 (1.5%, 3% or 4.5%) and maximum survivorship in M4 (50% to 85% in 5% increments) (Fig. 5.11). Survival in the post-spawning class PS was set to zero.

Once the logistic curve describing survivorship was selected, the resulting survival matrix S remained invariant for the duration of that particular simulation.

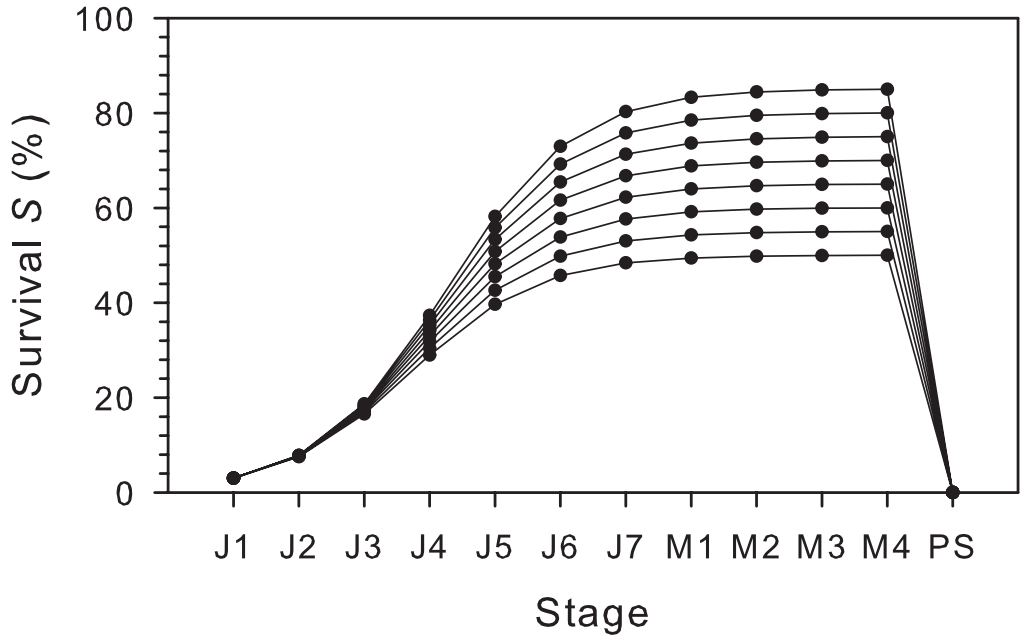


Fig. 5.11 Survivorship logistic curves with 3% minimum survivorship and a range of maximum survivorships (from 50% to 85% in 5% increments). Survival in the post-spawning class PS was set to zero. The same method was applied to calculate survivorship curves with 1.5% minimum survivorship and 4.5% minimum survivorship.

Simulations and model analyses

Incubation can take more than six months so two micro-cohorts are required to initiate the model run. Therefore, all simulations started with 1 million eggs in January and April 2005. For each scenario, the matrix population model followed the female population biomass and structure on a seasonal basis, from January 2005 to October 2070, which involved 264 three monthly steps.

The effect of survival on the population dynamics was investigated by visually comparing the seasonal population trajectory across the 65 years duration of the simulation. The survivorship scenarios that implied a

balance between stability and persistence were used in a comparison between the CC and noCC scenario. These comparisons included determining whether there were any systematic changes in which season dominated population numbers through time and whether different stages were dominant in different years. Sensitivity tests were also run to explore the elasticity of population size to survivorship. Elasticity was defined by Eq 17 (see Ch. 3 p. 74) and the elasticity of the seasonal population size through time to perturbation of ±1% in survivorship (Table 5.4) was calculated under both temperature scenarios.

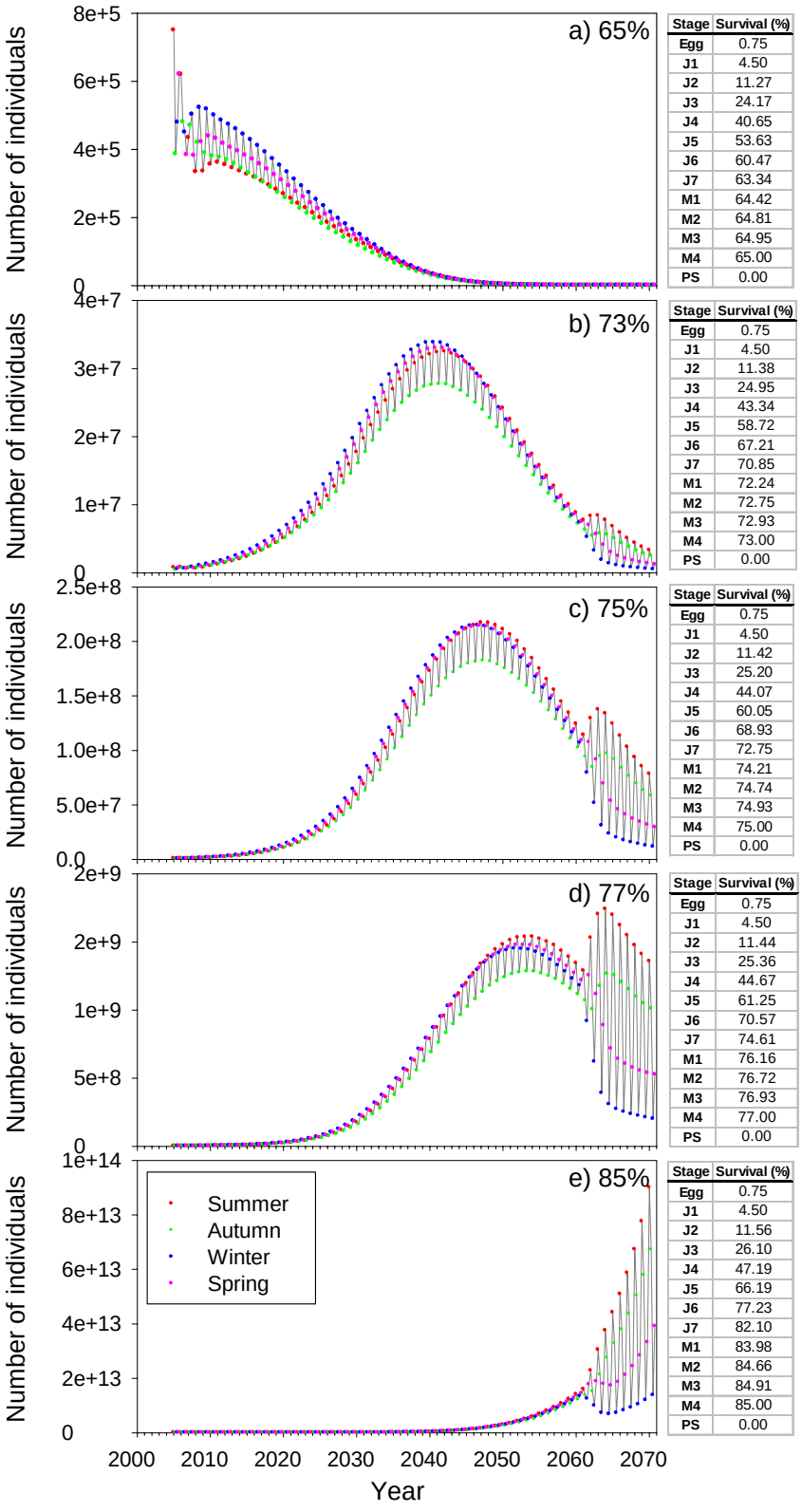
Table 5.4 Survivorship by stage used in the elasticity analysis. Survivorship was calculated as a ±1% change in survival at each stage, based on the 4.5% minimum/75% maximum survivorship curve.

	Survival		
Stage	**min 4.5%,max 75%**	**-1%**	**1%**
Egg	0.75	0.75	0.75
J1	4.50	4.46	4.55
J2	11.42	11.31	11.54
J3	25.20	24.94	25.45
J4	44.07	43.63	44.51
J5	60.05	59.45	60.65
J6	68.93	68.24	69.61
J7	72.75	72.02	73.47
M1	74.21	73.47	74.95
M2	74.74	73.99	75.49
M3	74.93	74.18	75.68
M4	75.00	74.25	75.75
PS	0.00	0.00	0.00

RESULTS

Effect of survival on the population dynamics

Survival curves using 1.5% and 3% as the minimum survivorship in J1 always resulted in an extinction of the simulated population by 2070. Survival curves using 4.5% as the minimum survivorship appeared more realistic. While maximum survivorship below 65% produced population extinction by 2070 (Fig 5.12a), maximum survivorship above 80% produced an exponential growth of the population (Fig 5.12e). Three survivorship curves that presented a balance between stability and persistence were selected (Fig 5.12b,c,d). All curves had a minimum survivorship of 4.5% but different maximum survivorship of 73%, 75% and 77% respectively (73% and 75% were selected as the population under 70% and 80% either failed to persist or exploded exponentially). The 75% maximum survivorship curve was used as the principal curve of interest for the remainder of the analyses, and was compared against the 73% and 77% maximum survivorship curves to detect any changes in seasonal dynamics through time.



Stage	Survival (%)
Egg	0.75
J1	4.50
J2	11.27
J3	24.17
J4	40.65
J5	53.63
J6	60.47
J7	63.34
M1	64.42
M2	64.81
M3	64.95
M4	65.00
PS	0.00

Stage	Survival (%)
Egg	0.75
J1	4.50
J2	11.38
J3	24.95
J4	43.34
J5	58.72
J6	67.21
J7	70.85
M1	72.24
M2	72.75
M3	72.93
M4	73.00
PS	0.00

Stage	Survival (%)
Egg	0.75
J1	4.50
J2	11.42
J3	25.20
J4	44.07
J5	60.05
J6	68.93
J7	72.75
M1	74.21
M2	74.74
M3	74.93
M4	75.00
PS	0.00

Stage	Survival (%)
Egg	0.75
J1	4.50
J2	11.44
J3	25.36
J4	44.67
J5	61.25
J6	70.57
J7	74.61
M1	76.16
M2	76.72
M3	76.93
M4	77.00
PS	0.00

Stage	Survival (%)
Egg	0.75
J1	4.50
J2	11.56
J3	26.10
J4	47.19
J5	66.19
J6	77.23
J7	82.10
M1	83.98
M2	84.66
M3	84.91
M4	85.00
PS	0.00

Fig 5.12 Seasonal population abundance under the CC scenario for various levels of survivorship: a) 4.5% minimum/65% maximum survival curve, b) 4.5% minimum/73% maximum survival curve, c) 4.5% minimum/75% maximum survival curve, d) 4.5% minimum/77% maximum survival curve and e) 4.5% minimum/85% maximum survival curve.

Octopus population under the climate change scenario

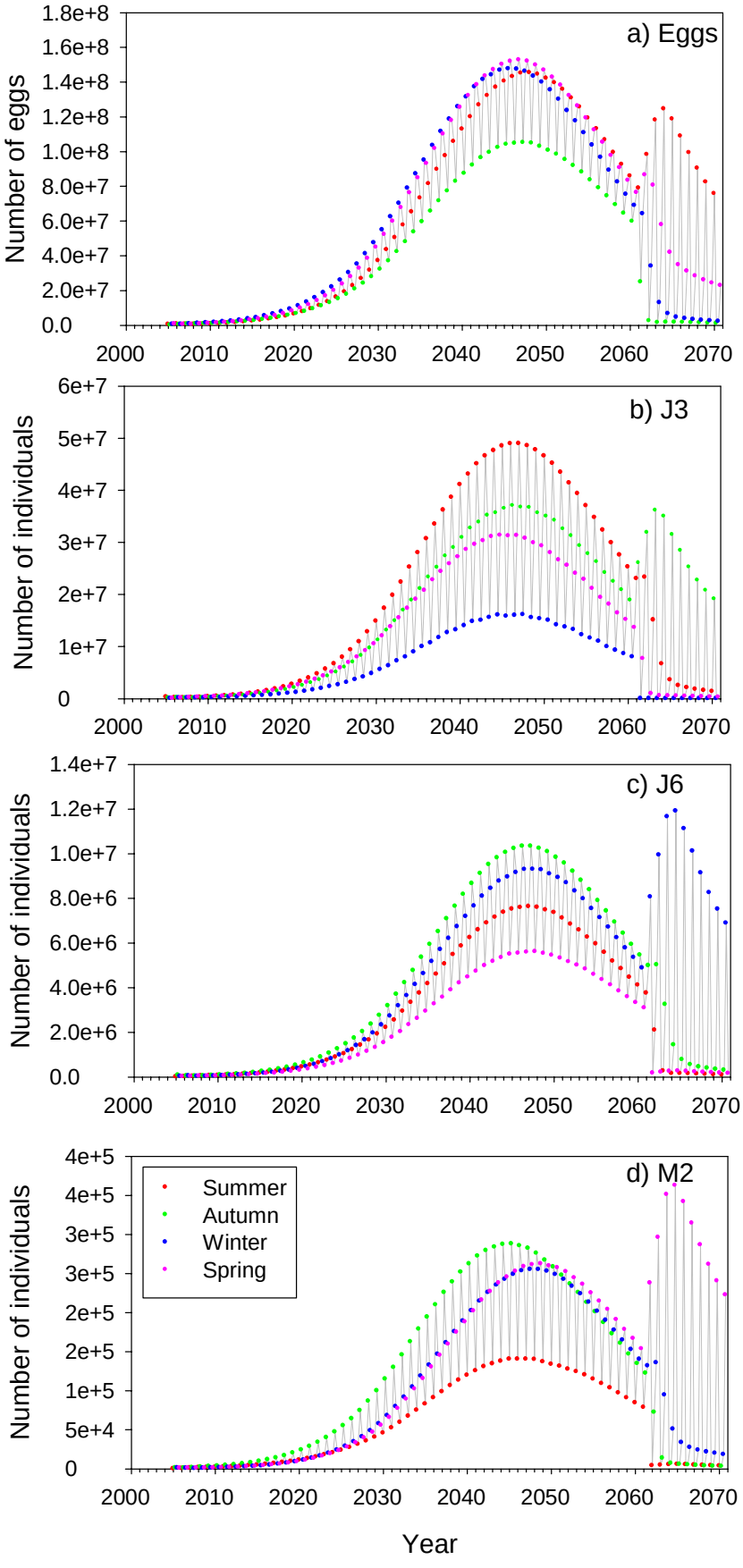
The fourth mature size class M4 was never populated during model runs and was therefore omitted from the results for clarity.

Population dynamics

The population trajectory under the 75% maximum survivorship followed a clear four phase pattern over the 65 years of the simulation, starting with an exponential growth in the population size until a maximum, followed by a short transition phase, leading to a subsequent exponential decrease in the population (Fig. 5.12c). The fourth phase (from here onward referred to as the "end phase") was more variable, exhibiting larger inter-seasonal fluctuations in population size than the other phases. The seasonal dynamics also changed with the various phases. During the exponential phase, population size always peaked in winter but shifted to peaking in summer past the transition phase, population size in winter becoming the least significant by the end of the simulation. Autumn contributed the least to the annual population through the first three phases but became the second highest contributor to the annual population in the end phase. The population size in spring remained between that of summer and winter throughout (Fig 5.12c). The seasonal dynamics under the 73% and 77% maximum survivorship curves were very similar to that of the 75% maximum survivorship curve.

The succession in seasonal dominance through time remained qualitatively identical. However, as survivorship increased, the population size during winter, spring and summer became increasingly similar until they were almost identical during the population exponential growth phase. Following the transition phase, the population size in these same three seasons became increasingly distinct during the exponential decline phase (Fig. 5.12b,c,d). Increasing survivorship increased the overall population size, delayed the onset of the exponential decline in the population and increased the seasonal fluctuations in population size during the end phase (Fig. 5.121b,c,d). The initiation of the end phase however appeared independent of survivorship, and always occurred in 2061.

The egg stage E, the hatchling stage J3, the juvenile stage J6, the mature stage M2 and the post-spawning stage PS contributed the most to the population dynamics and were analysed separately. As the results were similar under all three survivorship curves, only simulations for the 75% maximum survivorship are presented. Results suggested substantive phenological changes (i.e. changes in the timing of life-history events) over the 65 years of the simulation. Projections suggested a shift from a continuous egg laying pattern to seasonally restricted egg deposition (Fig. 5.13a). While eggs were present in all seasons at the beginning of the population exponential growth phase, eggs were only present in summer and to a lesser extend in spring by the end of the simulation.


a) Eggs
Number of eggs
1.8e+8
1.6e+8
1.4e+8
1.2e+8
1.0e+8
8.0e+7
6.0e+7
4.0e+7
2.0e+7
0.0
2000
2010
2020
2030
2040
2050
2060
2070
b) J3
Number of individuals
6e+7
5e+7
4e+7
3e+7
2e+7
1e+7
0
c) J6
1.4e+7
1.2e+7
1.0e+7
8.0e+6
6.0e+6
4.0e+6
2.0e+6
0.0
d) M2
4e+5
3e+5
2e+5
1e+5
5e+4
Summer
Autumn
Winter
Spring
Year

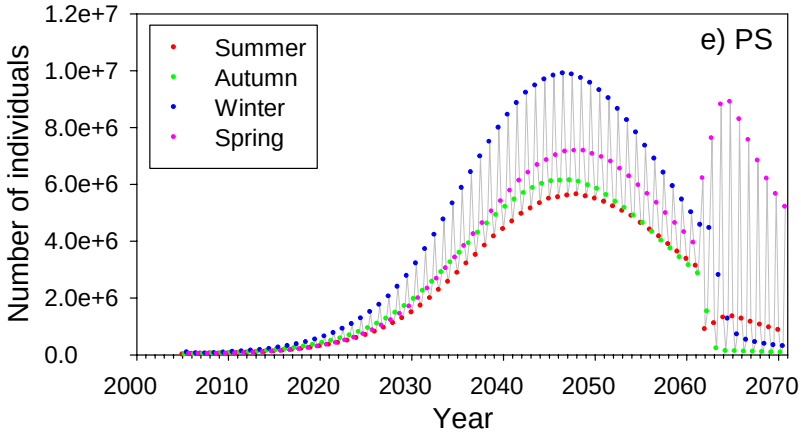


Fig 5.13 Seasonal abundance of a) eggs, b) hatchling stage J3, c) juvenile stage J6, d) mature stage M2 and e) post-spawning stage PS under the CC scenario with a 4.5% minimum/75% maximum survival curve.

Shifts in the seasons in which the different stages dominated population numbers were also evident, especially during the end phase (Fig. 5.13 and Fig 5.14). While seasonal dominance was stable for stages J3 (summer-autumn-spring-winter) and J6 (autumn-winter-summer-spring) throughout the population exponential growth and exponential decline, the seasonal dynamics changed dramatically in the end phase, with J3 hatchlings found almost exclusively in autumn (Fig. 5.13b) and J6 juveniles almost exclusively in winter (Fig. 5.13c); their numbers in other seasons declining to low levels by 2070. Mature stage M2 individuals were found predominantly in autumn and to a lesser extent in winter and spring (Fig. 5.13d). By the end of the exponential decline phase, M2 females were found in similar numbers in all three seasons, M2 population remaining lowest in summer. Beyond 2061, M2 population size peaked in

spring while their numbers dropped to low levels in other seasons during the end phase. A similar pattern was observed for the post-spawning females. PS females were found predominantly in winter throughout the population's exponential growth and exponential decline. Numbers of PS females in autumn were equivalent to that of spring during the exponential phase but declined to the lowest level by the end of the simulation (Fig. 5.13e). As for mature M2 females (Fig. 5.13d), numbers of PS females peaked in spring during the end phase while their numbers declined in other seasons.

Simulations also indicated a decrease in generation time (Fig. 5.14a,b and c), with spacing between peaks in abundance of eggs and abundance of post-spawning females of around 12 months during the population initial exponential growth phase reducing to 9 months during the end phase. Differences in the principal biological variables for females hatched in 2005 and 2070 are summarised in Table 5.5.

Table 5.5 Principal biological variables for females hatched in January 2005 and January 2070 under the CC scenario.

	Jan 2005	Jan 2070
Egg incubation (days)	186	97
Mean hatchling size A (g)	0.34	0.23
Mean body weight at reproduction B_{mat} (g)	466.0	395.8
Mean generation time (month)	12	9

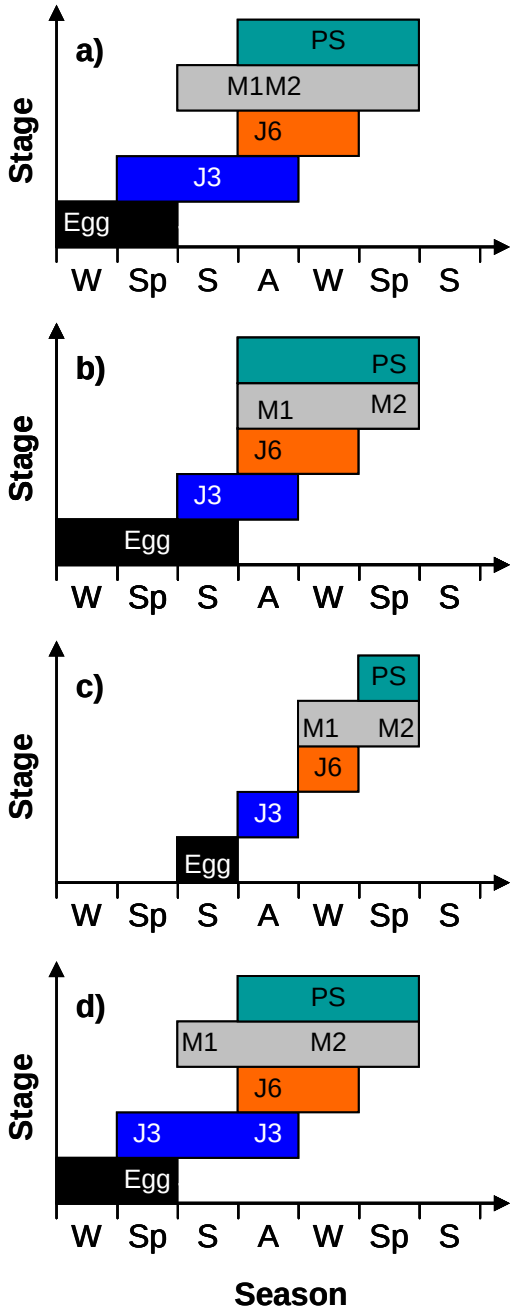


Fig. 5.14 Diagram of *Octopus pallidus* life cycle under a) the population exponential phase (CC scenario), b) the population exponential decline phase (CC scenario), c) the end phase (CC scenario), and d) the noCC scenario. Only the most significant seasons and stages are represented (i.e. eggs, hatchling J3, juvenile J6, mature females M1 and M2, post-spawning individuals PS). The intensity of the colour represent the periods of peak abundance (dark = abundant; light = low numbers). Survivorship was set as a 4.5% minimum/75% maximum survival curve.

Population structure

In order to compare and analyse the population structure through time, two specific years were selected to represent each phase, namely 2030 and 2040 for the population exponential growth phase, 2045 and 2050 for the transition phase, 2054 and 2058 for the exponential decrease phase and 2063 and 2068 for the end-phase. While the population structure during the exponential increase, transition and exponential decrease phases were relatively similar within seasons, the end phase exhibited a completely different population structure, and was therefore examined separately. As population structure followed a similar qualitative pattern under the three survivorship curves, only simulations for the 75% maximum survivorship are presented.

Excluding the dynamic in the end phase, size at hatching decreased with time, with a progressive increase in the proportion of smaller J1 and J2 hatchlings concomitant with a decline in the proportion of larger J3 and J4 hatchlings (Fig. 5.15). Large hatchlings (J4) were only present in significant numbers in summer and the juvenile stage J5 contributed little to the population. The proportions of the stages J6, J7 and PS remained approximately constant through time within a season (Fig. 5.15). Mature females constituted less than 1.1% of the total population at any time, and contributed on average 0.6%. The proportion of mature stages M1, M2 and M3 during autumn (Fig. 5.16) remained constant. Both winter and spring

exhibited an increase in the presence of smaller mature females (M1) and a decline in larger mature individuals (M3) (Fig. 5.16). Summer on the other hand, exhibited a decline in M1 females and an increase in the presence of M2 females, while the proportion of M3 females remained constant (Fig. 5.16).

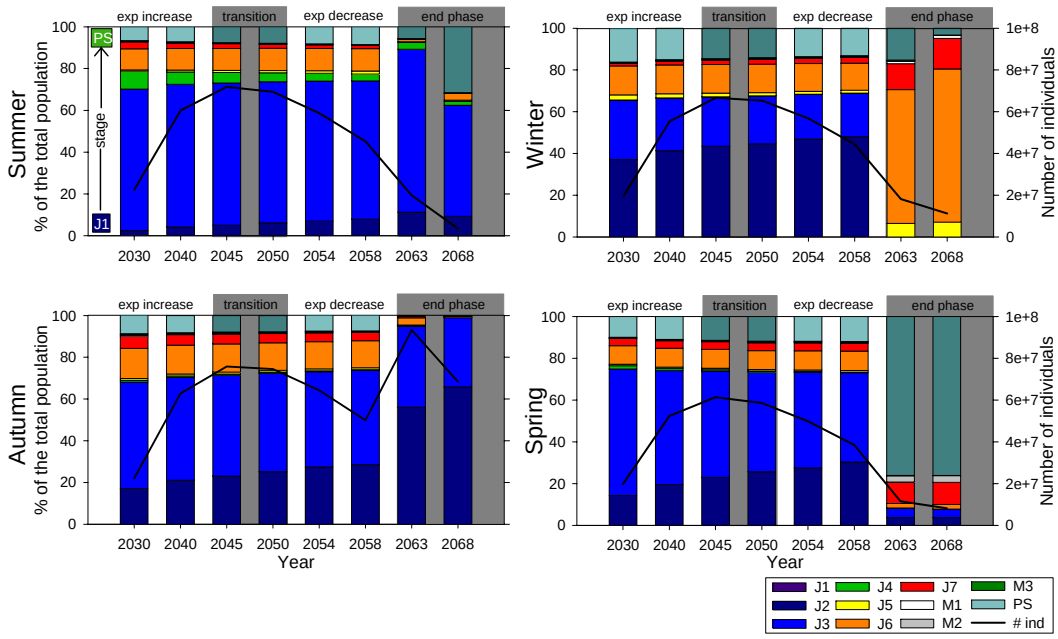


Fig. 5.15 Seasonal population structure for selected years under the CC scenario and a 4.5% minimum/75% maximum survival curve. Colours represent the proportion of each stage in the population and plain lines represent the total population size in the selected year.

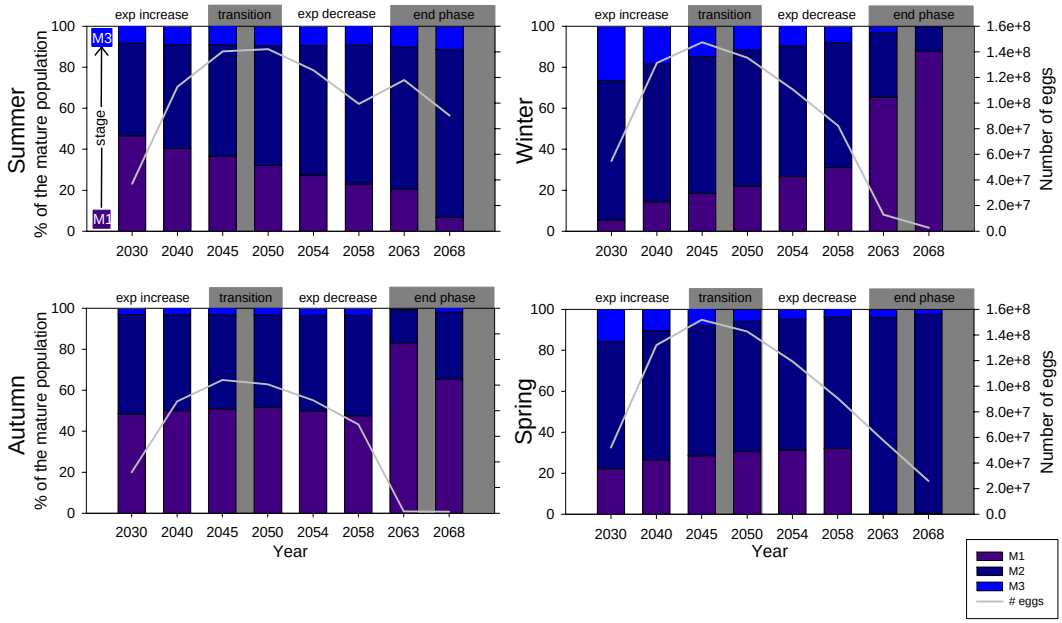


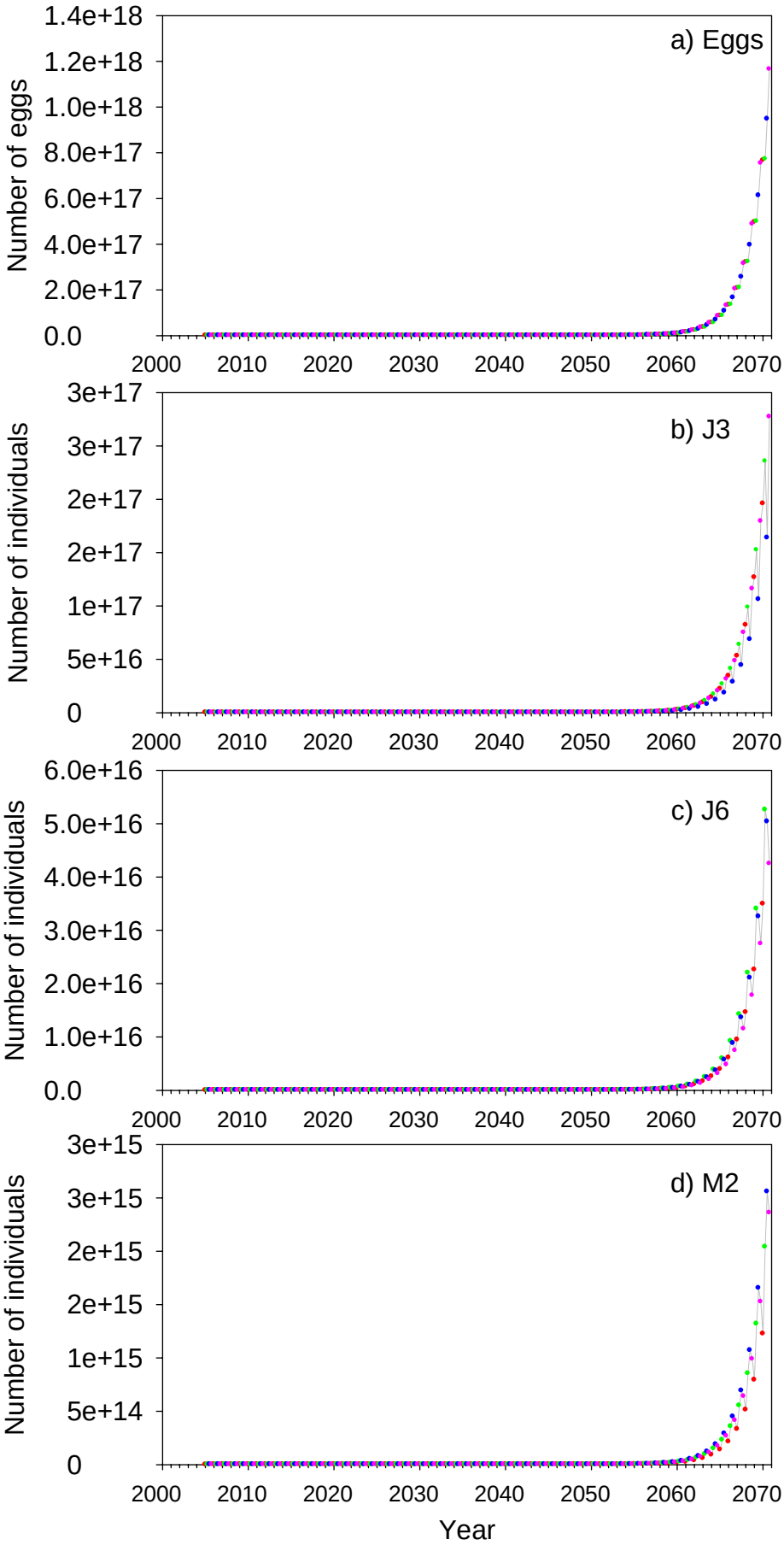
Fig. 5.16 Seasonal population structure for the mature stages in selected years under the CC scenario and a 4.5% minimum/75% maximum survival curve. Colours represent the proportion of the three mature stages in the mature female population and plain lines represent the number of eggs in the selected year.

During the end phase, the population structure changed dramatically. Few or no hatchlings were present in winter and spring, the population being dominated by juveniles and post-spawning individuals respectively (Fig. 5.15). Population structure in autumn, however, was almost exclusively composed of hatchlings, which contributed the most to the population size (Fig. 5.15). The proportion of mature females (all stages confounded) were extremely low (<0.15%) in summer and autumn and were at their highest in winter and spring (between 1.6% and 3.3%).

Octopus population under the no-climate change scenario

Population dynamics

The projected population grew exponentially throughout the 65 years of the simulation (Fig. 5.17) and presented similar patterns to the population exponential growth phase of the CC scenario (Fig. 5.14a and d). There were no changes in the seasons dominating population numbers in each stage through time, nor in the generation time of the species, which remained around 12 months (Fig. 5.14d).


a) Eggs
Number of eggs
1.4e+18
1.2e+18
1.0e+18
8.0e+17
6.0e+17
4.0e+17
2.0e+17
0.0
b) J3
Number of individuals
3e+17
3e+17
2e+17
2e+17
1e+17
5e+16
0
c) J6
Number of individuals
6.0e+16
5.0e+16
4.0e+16
3.0e+16
2.0e+16
1.0e+16
0.0
d) M2
Number of individuals
3e+15
3e+15
2e+15
2e+15
1e+15
5e+14
0
2000
2010
2020
2030
2040
2050
2060
2070
Year

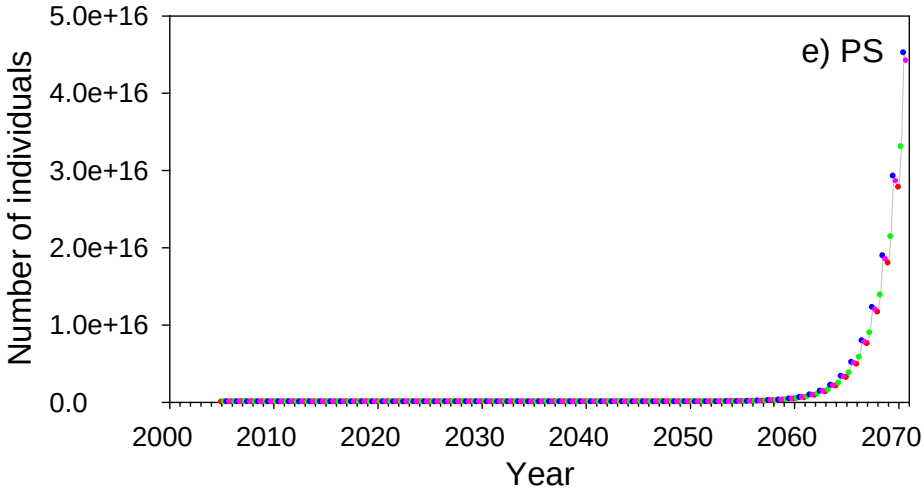


Fig. 5.17 Seasonal abundance of a) eggs, b) hatchling stage J3, c) juvenile stage J6, d) mature stage M2 and e) post-spawning stage PS under the noCC scenario with a 4.5% minimum/75% maximum survival curve.

Population structure

Population structure remained constant through time. Hatchlings contributed around 70% to the total population independent of the season, although the proportion of the various hatchling stages varied seasonally (Fig 5.18), with larger hatchlings (J3 and J4) dominating in spring and summer and smaller hatchlings (J2 and J3) in autumn winter. Mature females constituted between 0.70% and 0.85% of the total population depending on the season, with M2 females contributing the most (Fig. 5.19).

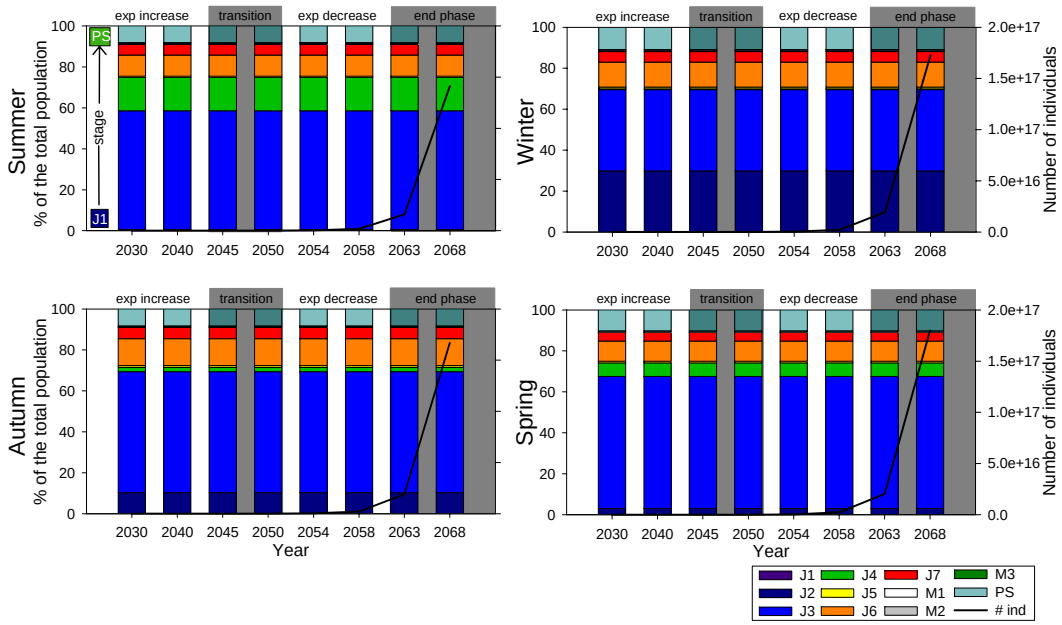


Fig. 5.18 Seasonal population structure for selected years under the noCC scenario and a 4.5% minimum/75% maximum survival curve. Colours represent the proportion of each stage in the population and plain lines represent the total population size in the selected year.

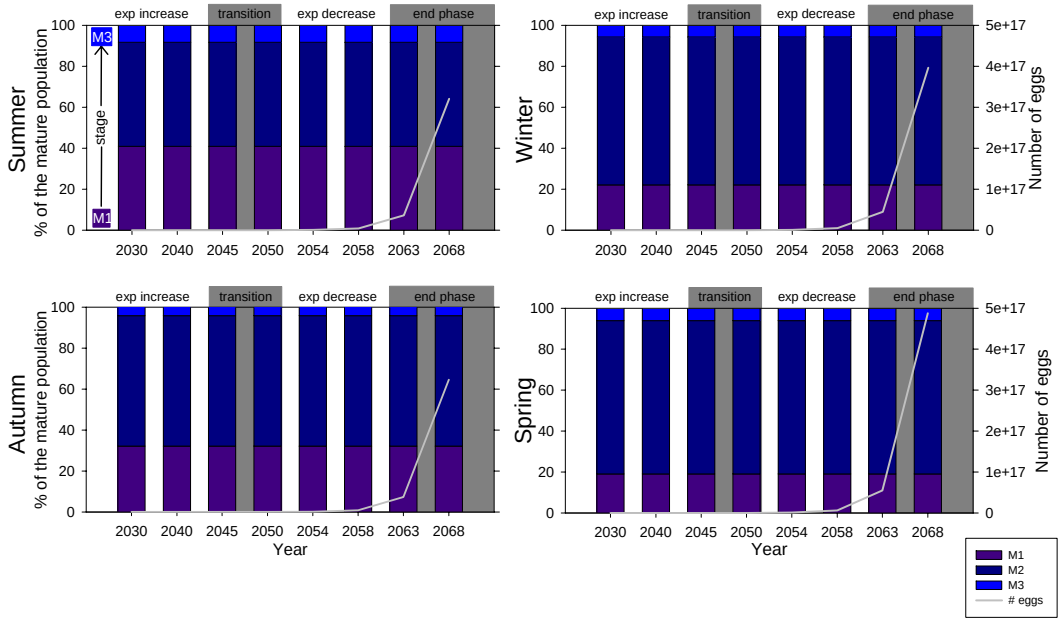


Fig. 5.19 Seasonal population structure for the mature stages in selected years under the noCC scenario and a 4.5% minimum/75% maximum survival curve. Colours represent the proportion of the three mature stages in the mature female population and plain lines represent the number of eggs in the selected year.

Elasticity analyses

Climate change scenario

The transition period (between the population exponential increase and exponential decrease phases) was slightly more sensitive to a 1% decrease in survival (*E*= -0.195%) than a 1% increase in survival (*E*= 0.147%). The end phase however always initiated in 2061, independent of the survivorship selected for the simulations. The population size was considerably more sensitive to an increase in survivorship, and sensitivity increased exponentially through time (Fig 5.20).

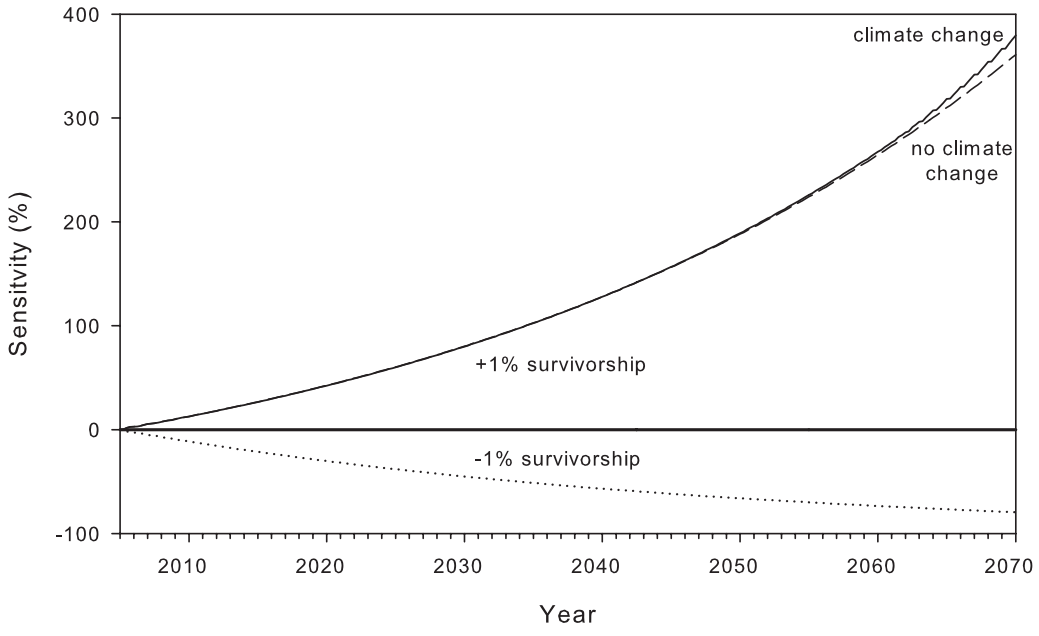


Fig. 5.20 Sensitivity of the population size through time to a 1% increase and 1% decrease in survivorship across all stages (based on the 4.5% minimum/75% maximum survival curve) under the CC scenario and the noCC scenario. Sensitivity at -1% for both scenarios were confounded.

No climate change scenario

As the population growth was exponential under this scenario, only the elasticity of the seasonal population size through time was tested. The population size was more sensitive to an increase in survivorship (Fig. 5.20) and sensitivities of the population size through time presented a very similar pattern to those under the CC scenario, the sensitivities at -1% survivorship being almost identical.

DISCUSSION

The population dynamics of pale octopus exhibited complex patterns and the predicted response of the Bass Strait population to climate change was non-linear. Increasing water temperatures may not be as beneficial to octopus as initially thought and projections suggest that the population would prosper more under a no climate change scenario. There is nevertheless scope for the population to thrive under climate change conditions, provided there is a sufficiently high survivorship. A minimum of 4.5 % survivorship for the juvenile stages and 70% for the largest mature stage were necessary in this model to ensure population survival in the selected time frame. Simulations and elasticity analyses suggest that the population dynamics are very sensitive to small increases in survivorship, a 1% increase in the survivorship of all stages resulting in a threefold increase in population size after 65 years, independent of the environmental temperature regime. At the level of population trajectory,

increased survivorship delays the transition from exponential population growth to exponential population decline, or even prevents the exponential decline altogether (i.e. beyond 80% maximum survivorship). Analysis of the population structure suggests that this threshold in the population abundance is caused by a simultaneous decrease in the number of traditionally larger mature females in summer and autumn, and an increase in the proportion of progressive smaller mature females in winter and spring. This progressive augmentation in the number of smaller mature females in the population through time would result in fewer eggs, as fecundity is related to body size in octopus (Mangold 1987), triggering a decline in population size. The sensitivity of the population to survivorship most likely stems from the very low proportion of mature females in the population (between 0.7% and 0.9% in the noCC scenario, and between 0.1% and 3.3% in the CC scenario) so that even a small increase in survivorship would have a large impact on the numbers of mature females in the population and consequently on the timing of the transition and on future population size and dynamics.

While the existence of a transition phase from population growth to population decline is a direct consequence of survivorship rates, the initiation of the end phase, and the ensuing changes in population structure and dynamics, is the result of the decrease in incubation time alone. Incubation times typically span over two seasons (four to six

months) but progressively warmer water temperatures bring the incubation time for eggs laid in summer down to around three months from 2061 in the simulations. As a consequence, eggs laid in spring and summer all hatch in autumn, producing an influx of hatchlings (J1, J2, J3) which dominate the population structure in that season. Following from that event, no hatchlings are found in winter, and the population is dominated by juveniles (J6 and J7) originating from the autumn cohort, which mature and deposit their eggs in spring. While some hatching still occurs in spring and summer, these cohorts become secondary to the large autumn cohort.

Through the 65 years of the simulation, a decrease in the species generation time from 12 to 9 months was also observed. As female octopus die after their brood hatch, the lifespan would consequently also be reduced from 12 to 9 months. This model suggests that the reduction in generation time was caused by the increase in water temperature, which is consistent with observations of shorter life spans at higher temperature for other benthic octopus species such as *Octopus bimaculoide*s (Forsythe and Hanlon 1988).

The combination of a declining generation time and events in the end phase lead to a streamlining of the life-cycle. Over time, pale octopus appears to move from aseasonal continuous recruitment with multiple micro-cohorts throughout the year, to a more restricted seasonal

recruitment with a main peak in autumn. This significant phenological change could potentially jeopardize the resilience of pale octopus to catastrophic events. For species with short annual or sub-annual lifespans, such as most cephalopods, the lack of overlap in generations means there is a need to reduce the risk of large scale mortality because of the absence of a recruitment buffer in the population (Warner and Chesson 1985; Moltschaniwskyj and Steer 2004). This is achieved by spatial risk spreading through migrations between feeding and spawning grounds (*Ommastrephes Bartramii*, Watanabe et al. 2008), or release of eggs (*Illex illecebrosus*, O'Dor 1998) or hatchlings (*Octopus vulgaris, Loligo vulgaris*, Moreno et al. 2009) into currents. Temporal risk spreading through egg deposition on a range of scales of weeks (Jackson and Pecl 2003) or months (Moltschaniwskyj and Pecl 2003) is another strategy, which can be concomitant with spatial risk spreading (*Sepioteuthis australis*, Moltschaniwskyj and Steer 2004). The pale octopus strategy is temporal, with spawning occurring all year round (Leporati et al. 2008a). The predicted reduction from several micro-cohorts to one main micro-cohort in autumn could result in a loss of resilience, with the risk of population collapse if the autumn cohort is subjected to catastrophic events. This is further aggravated by the limited movement capacity of this benthic species and the lack of immigration, a recent study suggesting that the eastern and western Bass Strait populations are discrete sub-populations (Doubleday et al. 2008). It is worth noting however that the resolution of

the present model is seasonal, so that only one cohort appears in autumn. Finer resolution might show the presence of weekly micro-cohorts throughout autumn, not dissimilar to aggregative spawning in squids (Jackson and Pecl 2003; Pecl and Jackson 2008), which would spread the risk of mortality and compensate to some extent for the reduction in the length of the recruitment period.

The predicted impact of climate change on the population dynamics of pale octopus presented in this chapter is likely to be conservative. For example, the east coast of Tasmania is predicted to undergo the greatest warming in the southern hemisphere, along with the south-east Australia region, due to a strengthening of the East Australian Current driven by a southward migration of the high westerly wind belt south of Australia (Hobday et al. 2006) (Fig. 5.21). Pale octopus populations in eastern Tasmanian regions are therefore likely to experience more extreme temperature variations than the western Bass Strait population from this study, and earlier changes and more aggravated impact on their population dynamics and structure can be expected.

Fig. 5.21 Major currents and circulation patterns around Australia. Climate change is predicted to strengthen the East Australian Current (EAC), increasing its southward flow to Tasmania. The yellow square represent the location of the studied pale octopus population. Figure adapted from Hobday et al (2008).

The simulations presented in this chapter constitute the first attempt to model the impact of climate change on a cephalopod population. While the model integrates an unprecedented level of complexity, results should be seen as qualitative rather than quantitative. The classical approach by which the population growth rate λ is studied (Caswell 2001) was not meaningful here as the transition matrices were not constant under the CC scenario (i.e. there were 264 transition matrices), and calculating λ for each transition matrix would not have been informative. As far as model structure is concerned, the present model represents a compromise between resolution and complexity. Analysing the population on a seasonal (3-monthly) basis is acceptable for a species with a life-span of 12 months but should be seen as the maximum time step necessary to analyse the population dynamics. A finer scale, in the order of one month, might

be preferable to capture more detailed dynamics but would significantly increase computing time and complexity and/or parameter estimation. Conversely, the number of size classes in the matrix population model might initially appear excessive but incorporating sufficient structure in the various stages is necessary to capture the dynamics (Benton et al. 2006). In the present model, all size classes were populated during the simulations (with the exception of the extremely large mature size class M4), indicating their necessity.

An important assumption of the model is that fisheries catches remain proportionally identical to the 2005/2006 catch levels, as the majority of the data utilised to construct this model are sourced from fisheries data from the Bass Strait pale octopus population. An increase in fishing pressure would equate to a lower survivorship, leading to earlier population decline than presented here and potential population collapse before 2070. Conversely, a reduction in fishing pressure would benefit the population by increasing the number of large juveniles and mature females in the population (pot selectivity in the fishery being >250g), hence delaying the population decline, eventually enough to push the population to exponential growth.

In order to grasp a better understanding of the population dynamics, future models should include catastrophic events in the projections.

Hatching success and adult survival in many cephalopod species are known to be affected by spikes in environmental temperature (Oosthuizen et al. 2002; Cinti et al. 2004) and abrupt changes in salinity (Paulij et al. 1990; Cinti et al. 2004; Sen 2005; Chapela et al. 2006). Such events are predicted to become more common under climate change conditions, with increases in the frequency of storm surges, floods and extremes in temperature in Australia (CSIRO 2007). The population rate of recovery will most likely depend of the frequency and timing of these catastrophic events and populations can be expected to be more resilient to perturbations occurring during the exponential growth phase rather then during the exponential decline phase.

While individual variability is indirectly integrated through parameterization with an individual-based bioenergetic model, the matrix population model is essentially deterministic. The inclusion of stochasticity would refine the projections to reflect more accurately the population dynamics. In the current model, fecundities are fixed for a particular mature size class (M1, M2 and M3) but these size classes span over 250g and fecundity is known to vary with body mass (Mangold 1987 and Fig. 5.8). While stochasticity could be included in diverse ways, randomly varying fecundity at size (F) could provide a relatively simple way to begin to capture known uncertainties into the model.

It is not clear for most cephalopod species whether there is any density dependence in recruitment or spawning success (Pierce et al. 2008), although studies of Lologinid squids suggest density-dependence effects on recruitment at least in specific populations (Agnew et al. 2000; Rodhouse 2001; Challier et al. 2006b). In the case of benthic octopus, which can feed indiscriminately on a variety of prey, density-dependence might come in the form of competition for appropriate brood sites rather than competition for food resources, although the latter can be expected in the case of exponential population growth. Given the lack of information, density-dependence was however not integrated in the model.

CONCLUSION

The model presented in this chapter constitutes the first attempt to model the impact of climate change on a cephalopod population. Simulations suggest that two main factors drive the population dynamics of pale octopus under the climate change scenario: survival and incubation time. While *Octopus pallidus* has the potential to be very prolific under climate change conditions, this adaptation may come at a cost. The population structure and dynamics are likely to change substantially, resulting in a potential decrease in generation time, streamlining of the life cycle and possible loss of resilience to catastrophic events.

Ch
6

General discussion

GENERAL DISCUSSION

The central aims of this thesis were to develop a series of models to describe individual growth in females as a function of size, individual variability, environmental temperature and nutrition; ultimately predicting the potential impact of climate change on the *Octopus pallidus* population in Bass Strait. In addressing these aims, this study is the first to 1) develop a mechanistic model to describe female octopus growth as a function of the main biotic and abiotic factors influencing cephalopod life history, 2) develop a stage-based approach to modelling the complete population dynamics of a cephalopod, 3) investigate the potential impact of climate change induced increases in sea temperature on the population structure and dynamics of a cephalopod species. The most important finding was that adaptation to climate change conditions is possible but may come at the cost of population resilience to environmental variability and catastrophic events. This study constitutes a first step towards the mechanistic modelling of the population dynamics of cephalopods as a function of environmental factors and a species' intrinsic characteristics. The model permits the exploration of the impacts of shorter term (e.g. El Niño) and longer term (e.g. climate change) environmental variations on cephalopod species of commercial importance.

Understanding the mechanisms of growth in any organism is essential not only to understand the current dynamics but also for any predictive work

on the future of a population. The work presented in this thesis provides new insights on the growth of octopus. Of particular interest is the observation that *O. pallidus* appears capable of substantial weight gain with little or no food consumption (Ch. 2), possibly as a result of the balance between the continuous hyperplasic and hypertrophic growth processes. This thesis also provides new substance to the debate of two-phase growth in cephalopods. The model results suggest that two-phase growth is not compulsory in juvenile octopus (Ch. 3 and Ch. 4) and that wild populations may in fact consist of a mixture of individuals displaying two-phase growth and exponential growth (Ch. 4), the proportion of which would varry with environmental temperature and food consumption. Overall, these findings highlight the ability of octopus to maximise the available resources to achieve maximum growth in a minimum amount of time, and could account for some of the variability in size observed in the wild. While we still do not fully comprehend growth processes in cephalopods, this research contributes to refining our understanding of the possible mechanisms involved.

As highlighted by Benton et al. (2006), there is a real need to develop models that can predict population dynamics in a changing world. In cephalopods, such models should ideally be based on some hypothesised mechanism relating abundance to the environment. However, this has so far proven difficult because of gaps in the knowledge of many cephalopod

species, especially of the early life stages during which environmental effects might be strongest (Pierce and Boyle 2003). The inclusion of individual variability also appears paramount considering the high levels of environmentally-induced plasticity observed in all aspects of cephalopods' life-cycle (Forsythe and Van Heukelem 1987; Boyle and vonBoletzky 1996; Forsythe et al. 2001a; Vidal et al. 2002), as well as the inherent growth plasticity displayed by individuals reared under identical conditions (see Ch. 2). The suite of models developed in this thesis represents a novel, mechanistic, method to model population dynamics in cephalopods. The strategy of using the results from a bioenergetics model to parameterise a matrix population model is powerful as it allows the indirect inclusion of individual variability as well as inferring transition probabilities (from one size class to another) that are not directly observable in nature.

As the first study to model the potential impact of climate change on a cephalopod species, this thesis has shown that the western Bass Strait *O. pallidus* population has the capacity to survive in warmer waters, and even thrive provided survivorship is sufficiently high. However, population persistence could come at the cost of a streamlining of the life cycle, with some micro-cohorts reaching their ecological limit and not persisting in the population, resulting in a general loss of resilience to catastrophic events. Much of the variation in population dynamics from the

simulations depended on the particular survivorship schedule used, and predictions from Ch. 5 have shown that a 21% change in maximum survivorship alone resulted in the difference between population extinction and population exponential growth. Simulations also revealed that a 1% increase in the survival rate for all stages would result in a doubling of the population size after three decades. This highlights that cephalopods are, and will remain, a volatile resource. Short generation time has been shown to be an advantage in cases of warming-related range shifts (Perry et al. 2005) and in response to changes in trophic structure (Caddy and Rodhouse 1998). Cephalopods may therefore become a successful group under climate change conditions. However, the low proportion of mature females in the population at any given time, combined with a predicted decrease in the numbers of large females as a result of rising temperatures, suggest a rapid population decline in the event of even a small increase in mortality.

In the context of climate change, survival in cephalopods is likely to be affected by two key factors that we are currently unable to predict: changes in ecosystem productivity and changes in the range and dominance of other species. Octopus (and cephalopods in general) are opportunistic animals that appear unselective in their choice of prey (Mather 1993; Boyle and Rodhouse 2005). It can therefore be argued that holobenthic cephalopods such as *O. pallidus* are less likely to be affected

than most other marine species by changes in ecosystem productivity as they can feed on a wide variety of prey. Whether food would be qualitatively sufficient is an open question, as low quality/digestibility might result in reduced growth (Villanueva 1994; García García and Aguado Giménez 2002) and an increase in energy expended on hunting would have repercussions on the energy budget. Merobenthic species (i.e. species with a planktonic phase such as *O. vulgaris*) are likely to be more sensitive than holobenthic species to changes in ecosystem productivity, at least during the paralarval stage. The survival of paralarvae depends largely on the presence of appropriate zooplankton prey in the water column (Perez and O'Dor 1998; Pierce et al. 2008), which in turn depends on phytoplankton abundance. Climate change is predicted to induce spatial, temporal and assemblage changes in marine primary productivity, through water acidification and changes in oceanic circulations (Hobday et al. 2006; Tunin-Ley et al. 2009). This will have important implications for survivorship of hatchlings and hence success of recruitment for these species.

Changes in species dominance and ranges as a consequence of climate change have already been observed in marine systems. Range expansion, poleward movements and/or shifts in depth of habitat have been observed in fishes (Dulvy et al. 2008), crustaceans (Panov et al. 2007), seabirds (Wynn et al. 2007) and cephalopods (Guerra et al. 2002; Zeidberg

and Robison 2007), with restructuring of marine assemblages in some areas. In the case of *O. pallidus*, extensive southwards movements towards higher latitudes are unlikely due to the limited dispersal capacity of this benthic species and its geographical location. Waters around Tasmania drop rapidly to depths of 5000m (see Fig. 1.2 in General Introduction). As Bass Strait is relatively shallow (<60m depth), movements to deeper water are only possible if the species moves further west, towards the continental shelf. It is therefore likely that pale octopus will remain in its present range and will see an influx of northern species arrive in its environment. The presence and settlement of invasive species (e.g. the European shore crab *Carcinus maenas*) has already been recorded in Tasmanian waters in the last decade (Hobday et al. 2008). The arrival of new competitors, predators and/or prey, will impact on survival, possibly differentially in the various size classes, with unpredictable consequences for the population dynamics of this species. High sensitivity of the pale octopus population to such changes in survivorship could mean population explosion, or disappearance of some of the sub-populations depending on the trophic level of the invading species and the geographical location of the octopus sub-population within Tasmanian waters.

While prey/predator dynamics will play a key role in determining endurance of cephalopod populations, they are only one of many factors

that will affect cephalopod survivorship. In the light of the potential decrease in resilience of cephalopod populations, a cautionary approach should be taken in the amount of fishing pressure applied to exploited stocks. Combinations of climatic events and over-fishing have already resulted in cephalopod population collapses (e.g. *Illex illecebrosus*, O'Dor and Dawe 1998; *Illex argentinus*, Nigmatullin et al. 2004) and predicted changes in the population dynamics due to climate change could jeopardize stock recovery in the future. The assumption that cephalopods will become a major fisheries resource, taking advantage of elevated temperature and changes in trophic structure to thrive, as has been observed for some species (e.g. *Dosidicus gigas*, Zeidberg and Robison 2007), should therefore be met with caution.

The models developed in this thesis focus on the impact of seawater temperature increase on the life history and population dynamics of octopus. The impact of ocean acidification, ensuing from an increase in CO_2 emissions in the atmosphere, was not included here because the predicted decrease in seawater pH is not expected to affect octopus significantly in the predicted acidification range (Zielinski et al. 2001). This may not however be the case for other cephalopods. Ocean acidification is likely to have a major impact on some species' metabolisms, and hence growth pattern (see Ch. 3). This is especially relevant for squids, whose oxygen extraction and energy production capabilities are severely

impaired at lower pH (Seibel and Fabry 2003; Pörtner et al. 2004; Rosa and Seibel 2008). Ocean acidification will also present a problem for many species forming shells or a skeleton from calcium carbonate minerals (mainly aragonite or calcite) as decreasing pH and CO_3^- ions concentrations result in a reduction in calcium carbonate saturation in seawater (Zeebe and Wolf-Gladrow 2001). However, the cuttlefish *Sepia officinalis*, with an aragonite-based internal shell, is not affected by prolonged exposure to elevated CO_2 levels in its environment, and does not exhibit a reduced growth or calcification rate within the range of CO_2 concentrations that elicits metabolic depression in most other marine invertebrates (Gutowska et al. 2008). The authors advanced the hypothesis that cephalopods might be characterised by a certain level of pre-adaptation to acidification and possess some form of buffer system, possibly as a response to the high CO_2 partial pressures in their blood encountered during exercise. Climate change, through ocean acidification, will therefore selectively advantage those species that can maintain an effective metabolism, such as octopus and cuttlefish species, potentially at the expense of squids. The impact of seawater acidification on cephalopods' calcium-based statolith, and the potential ensuing behavioural changes, are at this stage unknown.

Only the dynamics of female octopus were presented in this thesis. A model could not be developed for males as a consequence of the lack of

juvenile males in wild-caught samples. Female dynamics were based on the reasonable assumption that mature males of this species are always present in the environment to fertilise females (Leporati et al. 2008a). While this may well remain the case under a climate change scenario, it is likely that males will also undergo changes in their dynamics. Males in many cephalopod species, including *O. pallidus*, mature earlier than females (Jackson et al. 2005b; Watanabe et al. 2008), and at smaller body sizes in octopus (Silva et al. 2002; Leporati et al. 2008a). Increases in water temperatures could result, as with the predictions in females, in a reduction of the generation time and a streamlining of the life cycle, with the possibility of asynchrony between peaks in the abundance of mature females and mature males. Such differential changes in phenology between the sexes have been observed for terrestrial ectotherms, with changes in the timing of arrival to the breeding site as a result of climate change more pronounced in male than females newts (Chadwick et al. 2006). For *O. pallidus* in the present study, the lack of immigration of adults from adjacent regions could aggravate this potential issue. However, juvenile female octopus have the capacity to breed and store sperm until maturity (Mangold 1987; Rodríguez-Rúa et al. 2005), which may offset any asynchrony between the two sexes. Potential for decoupling of phenological relationships is speculative at this stage however and there is a need for a model representing male dynamics in octopus.

Questions have been raised as to whether cephalopod populations can be used as indicators of climate change (Jackson and Domeier 2003; Pierce et al. 2008). The results from this study, although based on one octopus species only, suggest that this may prove challenging and cephalopod abundance may not be a reliable measure. While some species may indeed increase in abundance due to elevated survivorship as a result of new favourable conditions (trophic changes, oceanography), others may decline due to unfavourable local conditions. Also, the response of cephalopod populations to climate change does not appear linear. Under some level of survivorship, an increase in water temperature can lead to a shift from population exponential growth to population exponential decline within a matter of years (namely the "transition phase" in Ch.5). The increasing incidence of catastrophic events (e.g. freshwater runoff from floods, spikes in temperatures, potentially more intense and common El Niño/La Nina events, Easterling et al. 2000), which were not included in the present simulations, would add to the already high fluctuation observed in cephalopod population abundance. The systematic examination of the life history characteristics (e.g. growth rates, hatchling size, fecundity, size at maturity) of specific populations, to detect trends of decreasing hatchling size and size at maturity, might be a better indication of climate change in the marine environment. The choice of which species/population could be used for this purpose is however speculative.

Cephalopods may just be too sensitive to environmental factors to be useful climate change indicators on their own.

APPLICABILITY TO OTHER SPECIES AND FUTURE STUDIES

The choice of pale octopus as a study species was intentional as the western Bass Strait population represented the simplest case scenario: a closed population of holobenthic octopus with little dispersion capacity. Applying this type of modelling to other cephalopods is possible but may require some modifications to the model structure. In any case, the essential requirements for successful modelling are a good understanding of the study species' life cycle, data for wild animals on hatchling size, size-at-age, size at maturity and fecundity, as well as feeding, oxygen consumption and growth data under various temperatures to establish the necessary relationships for the bioenergetic model. Special care should be taken in establishing the metabolic term for the energy balance equation (i.e. the function describing metabolic rate as a function of both temperature and body size), as this is likely to be the most influential term in the bioenergetic model (see Chapter 3). For squids, this might require the inclusion of an additional term to represent the depressing influence of decreasing seawater pH on metabolism.

Providing parameterisation with the appropriate data for the species, the model in its current form should be transferable to other holobenthic

octopus. Species with life cycles involving a paralarval stage (e.g. *Octopus vulgaris*, Caverivière et al. 2002) or migrations (*Sepia officinalis*, Dunn 1999; *Loligo gahi*, Arkhipkin et al. 2004) are more challenging to model and would require an adaptation of the model structure. Metapopulation models, a more complex form of matrix population models allowing the incorporation of spatial variation in the vital rates and processes (e.g. dispersal) that transfer individuals from one location to another (Caswell 2001) may be a more suitable model choice for species undergoing such movements. While modelling the population dynamics under the present environmental conditions may be achievable, modelling the potential impact of climate change requires predictions of the physical oceanography in the study area (i.e. temperature, but also pH and potential changes in currents). This is particularly relevant for species with a pelagic phase as changes in seasonal temperature and oceanic currents/upwellings have been linked to changes in paralarvae abundance (Otero et al. 2008) and migration of adults (Sims et al. 2001).

The modelling approach developed in this thesis is a first step towards modelling population dynamics of cephalopods as a function of environmental factors, but it may not be applicable to all species. Two-phase growth is the underlying assumption of the bioenergetic model and models developed in this study will therefore not be applicable to deep-sea cephalopods, argonauts and nautiluses, which are thought to have

different growth strategies (Boyle and Rodhouse 2005). While the concept of two-phase growth is applicable to squids, species that combine planktonic hatchlings, migrations between feeding and spawning grounds, and metabolic sensitivity to ocean acidification present extra modelling challenges. Future studies should focus on further testing this type of modelling approach on other species where extended biological and environmental datasets are available. Depending on the species characteristics and life history, the development of population dynamics models for males should be considered, in addition to that of females, to obtain a complete picture of the species population dynamics.

As highlighted in previous reviews (Rodhouse 2001; Pierce et al. 2008), the lack of information on the early life stages is problematic when attempting to model cephalopod life cycles. While the use of a bioenergetic model parameterised with laboratory and field data has largely circumvented this issue in the present study, any improvements on our understanding of the early juvenile phase would be beneficial. For most exploited species, this would include obtaining size-at-age information for individuals prior to their recruitment to the fishery as well as better characterising individual variability in inherent growth and hatch size. Such data would refine the model parameters and consequently our understanding of population structure and dynamics.

Embryonic incubation time and survivorship appeared as the two main factors affecting octopus populations under a climate change scenario. While the relationship between incubation duration and environmental conditions for cephalopods can be obtained from both laboratory (Sakaguchi et al. 1999; Steer et al. 2004; Sen 2005) and in-situ (Gowland et al. 2002b) studies, survivorship schedules under climate change scenarios are difficult to assess, particularly as they will largely depend on future predator/prey dynamics. Ecosystem models including a cephalopod component, such as those developed for the Northern Humboldt Current Ecosystem (Tam et al. 2008; Taylor et al. 2008), could provide some insight into future trophic dynamics for these species and refine predictions of population abundance under potential climate change scenarios.

Predicting the impact of climate change on marine ecosystems is challenging and nature is likely to surprise us with some unforseen dynamics in the coming decades. Cephalopods have the potential to adapt to climate change conditions but will remain a volatile resource, possibly even more so than today. Populations of the same species can be expected to respond in different ways depending on local environments and conditions, and mechanistic models relating cephalopod biology to the environment, like the one presented in this thesis, constitute a valuable way forward to elucidate population dynamics in these highly plastic animals.

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Effects of temperature on energetics and the growth pattern of benthic octopuses

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ABSTRACT: In octopus, growth trajectories have implications for survivorship, adult size and fecundity. Many species exhibit a 2-phase growth pattern starting with rapid exponential growth before shifting to a slower (commonly power) growth rate. Based on the concept that energy conservation enforces this threshold, we developed a temperature-dependent model which incorporates the energy balance between food intake and expenditure in growth and metabolism. We employed the model to investigate growth patterns occurring at different temperatures for 2 octopus species, *Octopus ocellatus* and *O. pallidus*. Model projections were consistent with laboratory data and suggest that increases in temperature as small as 1°C could have a significant influence on cephalopod growth, affecting the threshold body mass by up to 15.5% and the body mass at 100 d by up to 62.6%. Sensitivity analyses suggest that threshold size is more sensitive than threshold age to any given change in parameter values, and that metabolic rate has the greatest influence on the growth threshold. This model provides a basis for predicting individual growth trajectories and consequential population structure of natural octopus populations. This type of analysis also has the potential to predict optimum conditions for a species and could be a powerful tool for predicting how climate change might affect species distribution as well as population structure and abundance.

KEY WORDS: Energy balance · 2-phase growth · Gold-spot octopus · Pale octopus · Climate change

INTRODUCTION

Octopus are important ecological components of marine food webs, being simultaneously prey items, voracious predators and an increasingly important target for fisheries worldwide (Clarke 1996, Boyle & Rodhouse 2005, FAO 2005). One of the most remarkable characteristics of octopus are their energy efficiencies, which allows them to sustain high growth rates during their short lifespans (usually <18 mo) while maturing and reproducing. This is facilitated by a generalist diet, very high consumption rates, high conversion rates, efficient use of oxygen and their unique ability like most cephalopods to sustain continuous hyperplastic and hypertrophic muscle growth (Jackson & O'Dor 2001, Semmens et al. 2004). However, despite recent advances in this area (Wells & Clarke 1996, Daly & Peck 2000, Petza et al. 2006), our understanding of the energetics of octopus growth remains sketchy. There are still debates as to the actual form of the growth curve for wild octopus, in particular whether they display a 2-phase growth pattern (an initial rapid exponential phase followed by a slower second growth phase) as is often observed in captivity (Forsythe & Hanlon 1988, Domain et al. 2000, Semmens et al. 2004, Boyle & Rodhouse 2005). Analyses of field data may never shed light on this issue as field size-at-age data for highly variable species such as squid typically contain few data for the early part of the life span and frequently exhibit a greater scattering of data points with

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increasing age (Arkhipkin & Roa-Ureta 2005). This causes serious difficulties in statistical approaches that depend only on regression inference to estimate the individual growth curve, so that the curve may often be misspecified when data are inadequate to support the relationship being fitted. Grist & Jackson (2004) introduced the concept of energy balance as a mechanism that might lead to 2-phase growth in cephalopods. The authors hypothesised that after reaching a critical size, the energy intake from food would no longer sustain the energetic demands of both metabolism and individual growth at the current level. As a consequence, individuals are predicted to shift to a slower growth rate, thus resulting in a 2-phase growth pattern. While taking account of body size, this model does not explicitly invoke environmental temperature, which is the most important abiotic factor influencing cephalopod life history alongside nutrition. Since temperature influences all aspects of the energy budget and, according to the hypothesis of Grist & Jackson (2004), energetics determines the transition between the 2 growth phases, temperature must therefore influence the transition body mass and transition age out of exponential growth, and consequently individual growth trajectories. This has implications for survivorship (Calow 1987), adult size (Forsythe & Van Heukelem 1987) and hence fecundity (Mangold 1987) at the individual level, subsequently influencing population structure. Assessing the effect of temperature on the growth of octopus is therefore crucial to understanding the population dynamics of these short-lived and increasingly exploited species, particularly in the light of predicted warming of the oceans. Our main aim is to investigate the influence of temperature on the energetics of octopus, and its associated impact on growth, through the utilisation of a temperature-dependent energy balance model.

THE ENERGY BALANCE MODEL

Concept

The traditional formulation of the energy budget of marine animals is based on the balanced energy equation formulated by Winberg (1956), which follows the fundamental law of energy conservation

$$F_T = M + G + W \quad (1)$$

where F_T is the total energy intake rate from food, M and G are the respective rates at which energy is expended in metabolism and growth (both somatic and reproductive), and W is the rate at which energy is wasted in excretions such as urine, faeces and other wastage (e.g. mucus, shed sucker cuticles). In this paper, these rates are expressed in kJ d^{-1}. Unlike somatic growth, reproductive growth in octopus differs between sexes in both energy allocation and timing. Males appear to mature earlier, coinciding with the shift between growth phases, whereas females tend to mature in the second slower phase of growth (Semmens et al. 2004). Assessing reproductive investment has been achieved for a few species (Boyle & Knobloch 1984, Perez & Haimovici 1991, Cortez et al. 1995) but estimating the onset of sexual maturation remains problematic, as the influence of food availability and temperature on this aspect of reproduction has yet to be quantified. Given the deficiency in information, we did not incorporate reproductive growth to avoid introducing unsupportable complexity into the model. The current representation is consequently characteristic of females' energetics.

The rate W can be eliminated by way of an assimilation efficiency parameter A, defined as the proportion of the intake energy which is not lost in excreta (Kleiber 1947), so that

$$F_T \times A = F = M + G \quad (2)$$

In order for an individual to survive there must be sufficient energy available to support metabolism and growth so that $F \geq M + G$ or equivalently $F - M - G \geq 0$, which hence gives rise to an energy balance constraint (Grist & Jackson 2004).

The dependencies of metabolic rate M and food intake rate F on body mass B (in g) have previously been characterised by an allometric scaling law of the form $y = qB^p$ where $p > 0$ is a scaling exponent and $q > 0$ is a constant (West et al. 1997, Boyle & Rodhouse 2005, O'Dor et al. 2005). The growth rate G during the exponential phase is (by definition) directly proportional to body mass. Hence, the required supply of energy $E(B)$ can be expressed as a function of body mass B

$$\begin{aligned} E(B) &= F(B) - M(B) - G(B) \\ &= q_1 B^{p_1} - q_2 B^{p_2} - q_3 B \end{aligned} \quad (3)$$

where $E(B)$ must remain positive in order for an individual to survive (Fig. 1).

Beyond a critical body weight B^* achieved at age t^* (where $B^* = B_0 \exp(mt^*)$ and B_0 is the hatch size) when $E(B) = 0$, it follows that an individual would be unable to support its total energy expenditure. Grist & Jackson (2004) hypothesised that a shift from exponential growth would then be necessary.

The value of 0.75 has been traditionally assigned as the scaling exponent of metabolism p_2 for many animals (Kleiber 1932); however, octopus generally have higher p_2 values which may reach up to 0.90 (Katsanevakis et al. 2005). The q_i are generally species-specific (West et al. 1997) and are typically estimated from experimental studies.

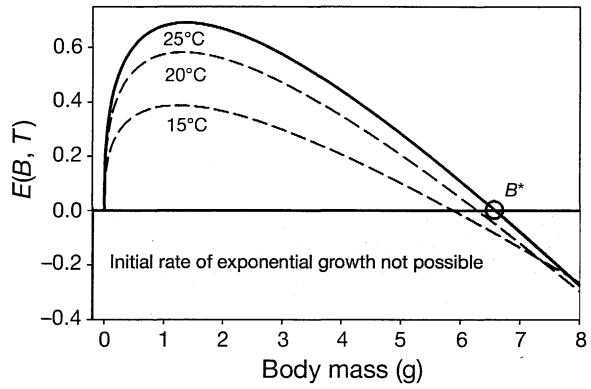

Fig. 1. *Octopus ocellatus*. Energy balance function $E(B,T)$ when parameterised for individuals reared at 15, 20 and 25°C with data obtained from Expt 1. By definition, threshold body mass B^* is reached when $E(B,T) = 0$

Incorporation of temperature dependence

Since temperature T affects feeding, metabolic and growth rates in cephalopods, we incorporate temperature dependency by modifying $E(B)$ to $E(B,T)$ and through specifying q_i as temperature dependent $q_i(T)$ so that

$$E(B,T) = F(B,T) - M(B,T) - G(B,T) = q_1(T)B^{p_1} - q_2(T)B^{p_2} - q_3(T)B \quad (4)$$

where the functions $q_i(T)$ were empirically determined from temperature-dependent data sets. We assume all body mass exponents p_i to be species-specific and independent of temperature as noted with p_2 by Zeuthen (1953), von Bertalanffy (1957) and Katsanevakis et al. (2005).

METHODS

We parameterised the model for 2 commercially exploited octopus, *Octopus ocellatus* and *O. pallidus*. Model parameters for each species were estimated from data published in the literature and collected in laboratory experiments, henceforth referred to as Expts 1, 2 and 3. Parameter values for both species are summarised in Table 1.

Data sets. Expt 1 provided data on the growth and feeding rates and oxygen consumption of *Octopus ocellatus*, details of which are published in Segawa & Nomoto (2002). Eleven juveniles hatched in captivity were reared for 205 d at 20 ± 1°C (n = 6) and 25 ± 1°C (n = 5). Individuals were fed hermit crabs *Clibanarius*

Table 1. *Octopus ocellatus* and *O. pallidus*. Parameter values for the temperature-dependent energy balance model. *B*: body weight (g), *T*: temperature (°C)

Eq.	Parameter	Value for *O. pallidus*	Value for *O. ocellatus*	Source
(9)	Growth rate: $k_3\,[m_{opt} - d \times (T_{opt} - T)^2]B$			
	Optimum temperature for growth (T_{opt}) (°C)	16.5	25	Present study[a], Segawa & Nomoto (2002)[b]
	Growth rate at T_{opt} (m_{opt}) (g d^{-1})	0.0167	0.0750	Present study[a,b]
	Parabolic constant (d) if $T \leq T_{opt}$	0.00039	0.00026	Present study[a,b]
	$T > T_{opt}$	0.00039	0.0015	Present study[a,b]
	Energy equivalent of octopus tissue (k_3) (kJ g^{-1})	4.05848	4.05848	O'Dor & Wells (1987)[a,b]
(11)	Feeding rate: $[f_{opt} - d_f \times (T_{fopt} - T)^2]B^{p1}$			
	Assimilation efficiency (A)	90%	90%	Wells et al. (1983)[a,b]
	Energy equivalent of food (k_f) (kJ g dry wt^{-1})	6.82353	11.05	Perez et al. (2006)[a], McKinney et al. (2004)[b]
	Conversion coefficient wet wt to dry wt ($k_{w/d}$)	0.249	0.339	Present study[a], McKinney et al. (2004)[b]
	Optimum temperature for feeding (T_{fopt}) (°C)	18.4	28.6	Present study[a,b]
	Feeding rate at T_{fopt} (f_{opt}) (kJ d^{-1})	0.584	1.064	Present study[a,b]
	Parabolic constant (d_f) if $T \leq T_{fopt}$	0.0083	0.0025	Present study[a,b]
	$T > T_{fopt}$	0.0276	0.0920	Present study[a,b]
	Feeding rate exponent (p_1)	1.17	0.39	Present study[a,b]
(12)	Metabolic rate: $k_1 \exp\left(a_2 + \frac{b_2}{T + k_2}\right)B^{p_2}$			
	Metabolic rate exponent (p_2)	0.88	0.81	Present study[a], Segawa & Nomoto (2002)[b]
	Conversion factor O_2 mg h^{-1} to kJ d^{-1} (k_1)	0.33758	0.33758	Prosser (1973)[a,b], Elliott & Davison (1975)[a,b]
	Conversion factor K to °C (k_2)	273.15	273.15	
	Constant (a_2)	21.80	21.80	Katsanevakis et al. (2005)[a,b]
	Constant (b_2)	−6952.8	−6952.8	Katsanevakis et al. (2005)[a,b]

[a]Reference for *O. pallidus*
[b]Reference for *O. ocellatus*

virescens and *Pagurus* spp. ad libitum. Individual food consumption was measured daily and octopus were weighed every 6 to 14 d to assess growth. The oxygen consumption curves provided the species-specific metabolic exponent p_2, which was calculated as the mean p_2 value obtained under the 2 temperature treatments. One individual in the 20°C treatment died at age 63 d and was excluded from the present analyses because there were too few data points to establish valid feeding and growth curves.

Expt 2 provided data on the growth rates and feeding rates of *Octopus pallidus*, details of which are published in André et al. (2008). Eight juveniles hatched in captivity were reared for 143 d at 14.7 ± 0.08°C (±SE) (n = 4) and 16.9 ± 0.12°C (n = 4). Animals were fed 2 porcelain crabs *Petrolisthes elongatus* daily, totalling between 4 and 12% of the octopus body weight d^{-1}. The level of food offered was comparable with the level of food consumed by other octopus species reared in captivity under ad libitum conditions (Joll 1977, Mangold 1983, O'Dor & Wells 1987) and the survival rate over the duration of the experiment was 75% (with 2 individuals dying before the end of the experiment in the warm treatment). Individual food consumption was measured daily and octopus were weighed every 5 to 10 d to assess growth. One individual in the 16.9°C treatment was excluded from the analyses as it died at age 57 d and there were too few data points to establish valid feeding and growth curves.

Expt 3 provided data on the metabolism of *Octopus pallidus*. Oxygen consumption at 18°C was measured at ages 93, 132 and 146 d for 2 randomly selected individuals from Expt 2. The resulting curve provided the species-specific metabolic exponent p_2. Further details of the experimental procedures are presented in Appendix 1.

Experimental estimation of transition body mass and age. We used the method of Hatfield et al. (2001) based on instantaneous relative growth rate (IRGR) to identify the transition point between the growth phases. If growth is exponential, IRGR (i.e. % increase in body mass d^{-1}) will remain constant from measurement to measurement, although there will be some fluctuation as in any biological system (Hatfield et al. 2001). The point at which IRGR starts to decline steadily marks the end of the initial exponential growth phase. The instantaneous growth rate for cephalopods following exponential growth is typically calculated according to the equation:

$$\mathrm{IRGR} = \left(\frac{\ln B_2 - \ln B_1}{t_2 - t_1}\right) \times 100 \quad (5)$$

where B_2 is the body mass at time t_2 and B_1 is the body mass at time t_1 (Forsythe & Van Heukelem 1987).

Using this method, we clearly identified a 2-phase growth pattern for *Octopus ocellatus* individuals in Expt 1 (Fig. 2) with a mean ± 95% CI threshold age t^* of 43 ± 27 d at 20°C (range = 15 to 71 d, n = 5) and 37 ± 12 d at 25°C (range = 25 to 49 d, n = 5), and a mean ± 95% CI threshold body mass B^* of 2.5 ± 3.5 g at 20°C (range = 0 to 6.0 g, n = 5) and 2.3 ± 1.6 g at 25°C (range = 0.7 to 3.9 g, n = 5). No threshold was detected for *O. pallidus* in Expt 2 as growth remained exponential during the duration of the experiment (Fig. 2).

Model parameterisation. ***Growth rate:*** Growth studies have long established that temperature strongly influences the growth rate of cephalopods (e.g. Mangold & von Boletzky 1973, Forsythe & Hanlon 1988, Leporati et al. 2007, André et al. 2008). The dependence of growth rate on temperature in fish has been modelled with an inverted parabola to represent the general nonlinear decrease in growth rate observed towards extreme temperatures (e.g. Ricker 1979, Bartsch 2002). This model has a central optimum, corresponding to the maximum growth rate, and a symmetrical drop-off on both sides. Based on this inverted parabolic function, the temperature mediation of growth rate coefficient m is given by:

$$m(T) = m_{\mathrm{opt}} - d(T_{\mathrm{opt}} - T)^2 \quad (6)$$

where m_{opt} is the maximum value of $m(T)$ at the optimum temperature, d is a constant, T_{opt} is the optimum temperature for maximum growth and T is the ambient temperature. However, T_{opt} may not necessarily be the midpoint of the species' temperature range so that asymmetric curves might follow from introducing temperature limits on either side of the optimum (Bartsch 2002). The temperature-dependence of growth rate is then expressed by 2 equations:

$$\begin{aligned} m(T) &= m_{\mathrm{opt}} - d_1(T_{\mathrm{opt}} - T)^2 \quad T < T_{\mathrm{opt}} \\ &= m_{\mathrm{opt}} - d_2(T_{\mathrm{opt}} - T)^2 \quad T > T_{\mathrm{opt}} \end{aligned} \quad (7)$$

During exponential growth at constant temperature, instantaneous growth rate (in g d^{-1}) is given by

$$G(B) = \frac{\mathrm{d}B}{\mathrm{d}t} = mB_0 \exp(mt) = mB \quad (8)$$

This can be expressed in terms of its energy equivalent (in kJ d^{-1}) as a function of body mass with temperature dependence incorporated from Eq. (6) to obtain

$$G(B,T) = q_3(T)B = k_3 m(T)B = k_3[m_{\mathrm{opt}} - d(T_{\mathrm{opt}} - T)^2]B \quad (9)$$

where k_3 is the kJ energy equivalent of 1 g of octopus tissue.

To estimate early post-hatch growth rate m at different environmental temperatures, we performed, for

each temperature treatment (warm or cool) and each species, a regression of body mass versus time using nonlinear mixed-effect models with an exponential model $B = B_0 \exp(mt)$ (Fig. 2, Table 2). This standard approach for repeated measures uses maximum likelihood estimation with an underlying assumption that individual data are normally distributed to determine parameter estimates (Lindstrom & Bates 1990).

For *Octopus ocellatus*, the regression was only performed up to the mean threshold point, after which octopus entered a slower growth phase. We assumed the growth rate m to be 0 at the lower and upper limit of a species' thermal range, namely 10 and 23°C for *O. pallidus*, and 8 and 32°C for *O. ocellatus*. For *O. pallidus*, we obtained the parameters m_{opt}, T_{opt} and d by nonlinear regression of an inverted parabolic curve (Eq. 6) to the combined data sets of 'growth rate versus temperature' data pairs from Expt 2 and the 2 'zero growth rate versus temperature' data pairs estimated from the thermal range.

For *Octopus ocellatus*, we estimated m_{opt} to be the maximum growth rate observed in Expt 1 (0.075 g d^{-1} with corresponding T_{opt} of 25°C), which resulted in an asymmetrical inverted parabolic curve for temperature-dependence (Eq. 7). Parameter d_1 was obtained from nonlinear regression of an inverted parabolic curve to the point pair (m_{opt}, T_{opt}) and the 'zero growth rate versus temperature' data pairs (0,8) and (0,42).

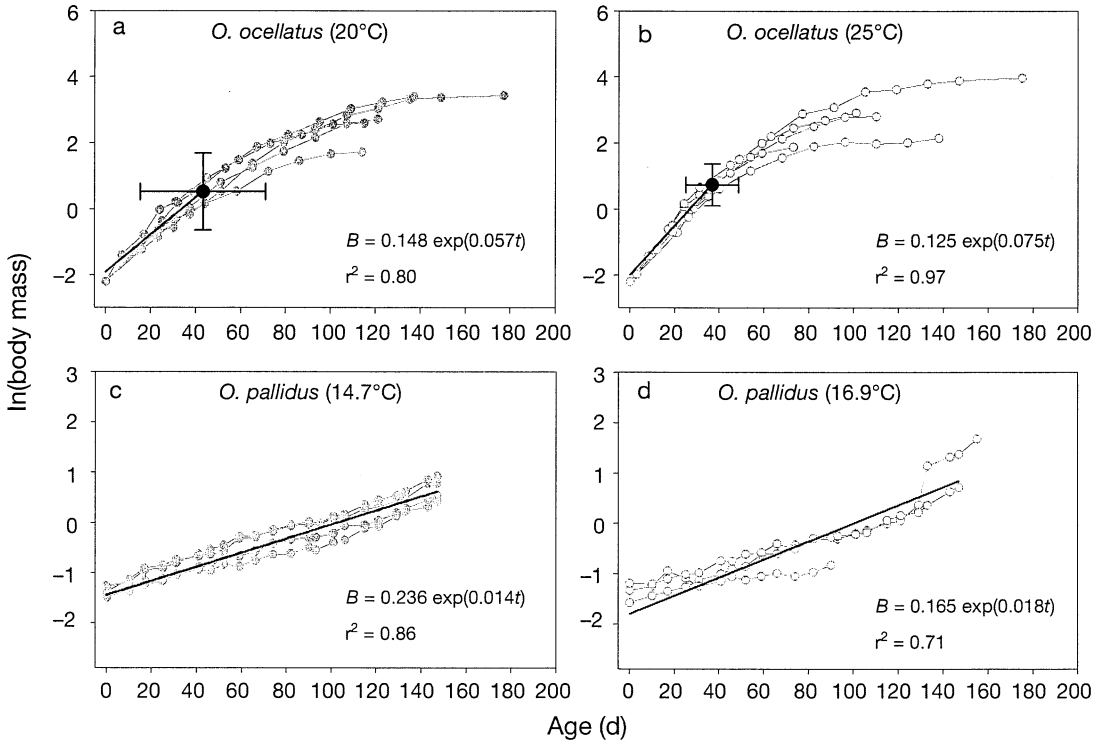

Fig. 2. *Octopus ocellatus* and *O. pallidus*. Individual growth curves for *O. ocellatus* at (a) 20°C (n = 5) and (b) 25°C (n = 5), and *O. pallidus* at (c) 14.7°C (n = 4) and (d) 16.9°C (n = 3). The solid black lines, estimated from nonlinear mixed-effect models, represent the mean growth curve for the initial growth phase and the black dots represent the mean transition age and body mass (±95% CI) out of the exponential growth phase

Table 2. *Octopus ocellatus* and *O. pallidus*. Feeding rate and growth parameters with associated SE estimated by nonlinear mixed-effect models

Species	Temperature (°C)	*Feeding rate:* $F = q_1 B^{p_1}$ $q_1 \pm$ SE	$p_1 \pm$ SE	*Growth:* $B = B_0 \exp(mt)$ $B_0 \pm$ SE	$m \pm$ SE
O. ocellatus	20.0	0.778 ± 0.0402	0.46 ± 0.0223	0.148 ± 0.0192	0.057 ± 0.0047
	25.0	1.117 ± 0.1316	0.31 ± 0.0444	0.125 ± 0.0128	0.075 ± 0.0039
O. pallidus	14.7	0.464 ± 0.0300	1.206 ± 0.1453	0.236 ± 0.0237	0.014 ± 0.0003
	16.9	0.517 ± 0.0451	1.126 ± 0.0912	0.165 ± 0.0648	0.018 ± 0.0073

Parameter d_2 was obtained from nonlinear regression of an inverted parabolic curve to the point pair (m_{opt}, T_{opt}) and the 'zero growth rate versus temperature' data pairs (0,18) and (0,32). We assumed coefficient k_3 for both species to be the same as for *O. cyanea*, which we sourced from O'Dor & Wells (1987).

A plot of the temperature-dependence of growth rate for both species is represented in Fig. 3.

Feeding rate: From Expts 1 and 2, we estimated individual feeding rate F (in kJ d^{-1}) every 5 to 14 d over the duration of the experiments using the formula:

$$F = F_w A k_f k_{w/d} \quad (10)$$

where F_w is the feeding rate in g wet wt d^{-1}, A is the assimilation efficiency, k_f is the energy equivalent of the prey tissue in kJ g^{-1} dry wt and $k_{w/d}$ is the wet weight to dry weight conversion coefficient for prey tissue. For both octopus species, we used the general cephalopod A = 90% from Wells et al. (1983). The k_f for porcelain crabs was sourced from Perez et al. (2006) and we estimated $k_{w/d}$ from the wet:dry weight ratio of 30 crab samples from Expt 2. We used the values of k_f and $k_{w/d}$ estimated by McKinney et al.(2004) for the hermit crab *Pagurus longicarpus* in lieu of the other hermit crab species (*Pagurus* spp. and *Clibanarius virescens*). We performed regressions of feeding rate versus body mass using a nonlinear mixed-effect model with a power model $F(B) = q_1 B^{p_1}$ for each species and temperature treatment (warm or cool) (Fig. 4, Table 2).

Higher temperatures result in higher feeding rates in octopus (Mangold & von Boletzky 1973, Van Heukelem 1973, Mangold 1983, Segawa & Nomoto 2002, André et al. 2008). Towards the maximal thermal tolerance of a species, however, the feeding rate starts to decline (Mangold 1983). We therefore assumed the relationship between q_1 and temperature to be an asymmetrical inverted parabola as for growth rate so that:

$$F(B,T) = q_1(T) B^{p_1}$$

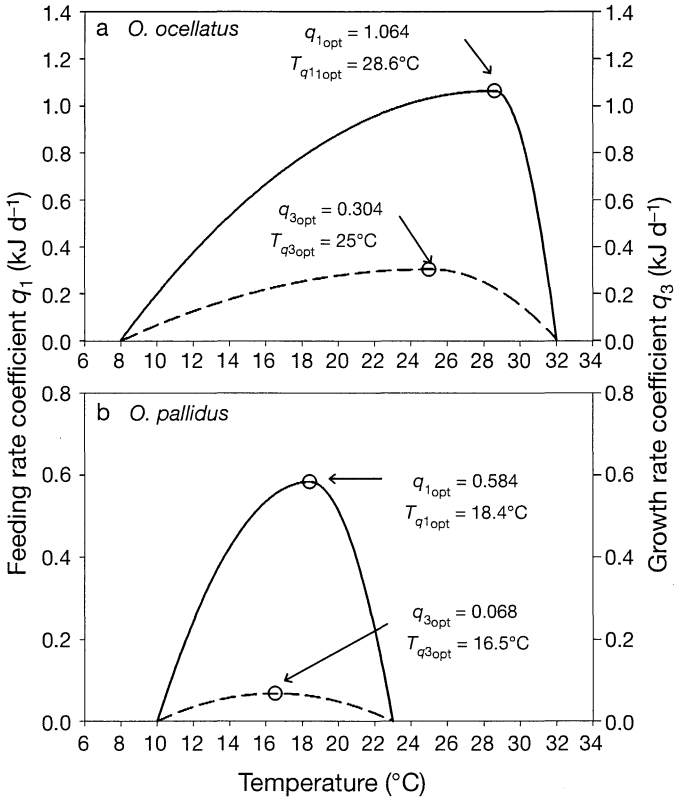

Fig. 3. (a) *Octopus ocellatus* and (b) *O. pallidus*. Feeding rate coefficient q_1 (solid line) and the growth rate coefficient q_3 (dashed line) as a function of temperature T. For each species, symmetric or asymmetric inverted parabolic curves were used to describe $q_1(T)$ and $q_3(T)$ across the thermal range encountered in nature

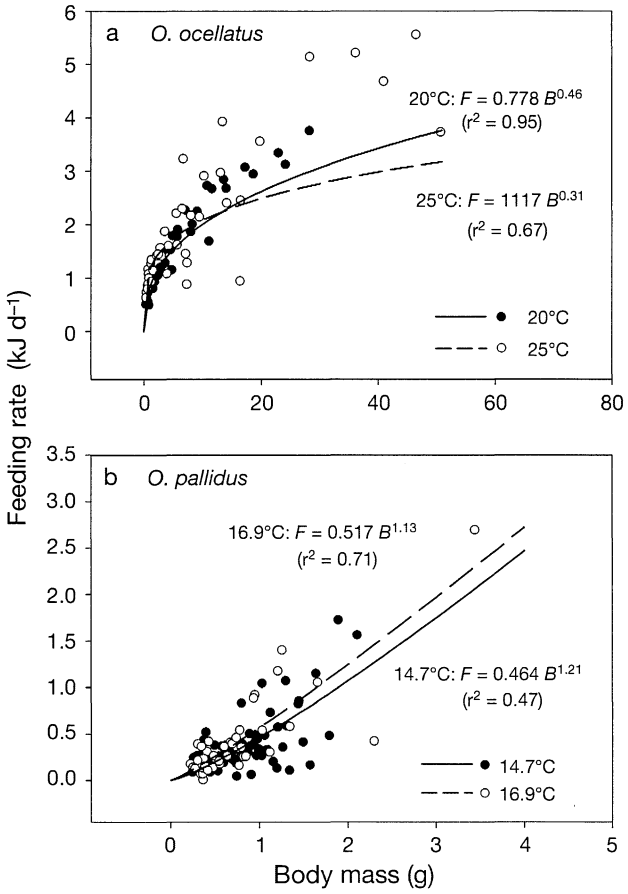

Fig. 4. *Octopus ocellatus* and *O. pallidus*. Feeding rate F as a function of body mass B estimated from nonlinear mixed-effect models for (a) *O. ocellatus* at 20°C (solid line, n = 5) and 25°C (dashed line, n = 5) and (b) *O. pallidus* at 14.7°C (solid line, n = 4) and 16.9°C (dashed line, n = 3)

with

$$q_1(T) = f_{opt} - d_{f1}\left(T_{f_{opt}} - T\right)^2 \quad T < T_{f_{opt}}$$

$$= f_{opt} - d_{f2}\left(T_{f_{opt}} - T\right)^2 \quad T > T_{f_{opt}} \qquad (11)$$

where T_{fopt} is the optimum temperature for maximum feeding rate f_{opt}, d_{f1} and d_{f2} are constants and T is the ambient temperature. We assumed the difference between T_{opt} and T_{fopt} to be relative to the species' thermal range and proportionally constant between octopus species. Based on known thermal range and T_{opt} of our study species and data for *Octopus vulgaris* (thermal range: 12 to 29°C, T_{opt} = 17.5°C, T_{fopt} = 20°C) from Aguado Giménez & García García (2002), we estimated T_{fopt} to be 28.6°C for *O. ocellatus* (thermal range: 8 to 32°C, T_{opt} = 25°C) and 18.4°C for *O. pallidus* (thermal range: 10 to 23°C, T_{opt} = 16.5°C). We performed a nonlinear regression of the inverted parabolic curve to the experimental 'feeding rate versus temperature' data pairs, setting the 'zero feeding rate' at 8 and 49.2°C for *O. ocellatus* and 10 and 26.8°C for *O. pallidus*. The maximum feeding rate f_{opt} and constant d_{f1} that minimised the sum of squares to the feeding rate data were retained for each species. The constant d_{f2} was then obtained from nonlinear regression of an inverted parabolic curve to the point pair (f_{opt}, T_{fopt}) and the 'zero growth rate versus temperature' data pairs (0,25.2) and (0,32) for *O. ocellatus*, and (0,13.8) and (0,23) for *O. pallidus*. A plot of the temperature-dependence of feeding rate for both species is represented in Fig. 3.

Metabolic rate: Temperature and body mass are the 2 most important factors linked to metabolic rate (Gillooly et al. 2001). Katsanevakis et al. (2005) developed a model of the form $M(B,T) = q_2(T)B^{p_2}$ to encompass the effect of both these factors on the oxygen consumption rate of *Octopus vulgaris*, and suggested that the term $q_2(T)$ could be generalised because metabolic rates of octopod species have a similar dependence on temperature. To obtain metabolic rate in kJ d^{-1} as a function of temperature in °C, we re-expressed the equation of Katsanevakis et al. (2005) as:

$$M(B,T) = q_2(T)B^{p_2} = k_1 \exp\left(a_2 + \frac{b_2}{T + k_2}\right)B^{p_2} \qquad (12)$$

where M is the oxygen consumption rate in kJ d^{-1}, B is the body mass, T is the temperature in °C, k_1 is the conversion factor from mg h^{-1} to kJ d^{-1}, k_2, a_2 and b_2 are constants and p_2 is a species-specific metabolic rate exponent. Parameter values for a_2 and b_2 were imported from Katsanevakis et al. (2005). We estimated p_2 from Expt 1 for *O. ocellatus* and Expt 3 for *O. pallidus*. Coefficients k_1 and k_2 were obtained from the literature (Prosser 1973, Elliott & Davison 1975). Since the original formula was tested in the temperature range 13 to 28°C (Katsanevakis et al. 2005), we determined the function $q_2(T)$ across the temperature ranges 13 to 28°C for *O. ocellatus* and 13 to 23°C for *O. pallidus* to avoid extrapolation.

Model estimation of transition body mass and age. We compared the threshold body mass B^* and age t^* estimated experimentally with model growth projections for B^* and t^* at the experimental rearing temperatures of 20 and 25°C for *Octopus ocellatus* and 14.7 and 16.9°C for *O. pallidus*.

The relationship between growth pattern and temperature was explored by plotting B^* and t^* as functions of temperature between the ranges of 13 and 23°C for *Octopus pallidus* and 13 and 28°C for *O. ocellatus*. Additionally, we projected growth trajectories over 100 d with individuals starting from the same hatch size B_0, but experiencing different temperature scenarios. We estimated growth trajectories every degree between 13 and 28°C for *O. ocellatus* and 13 and 23°C for *O. pallidus*. In this simple simulation, growth was assumed to be exponential in form until the transition point. The second slower growth phase was represented as linear and tangential to transition point (t^*, B^*). Hatch size B_0 was representative of the species and was set to 0.11 g for *O. ocellatus* (Segawa & Nomoto 2002) and 0.25 g for *O. pallidus* (Leporati et al. 2007).

Sensitivity analysis. A sensitivity analysis was performed to assess the response of model growth projections to small changes in parameter values. We used the metric of 'elasticity', in which the effect of proportional (rather than absolute) perturbations on a given output quantity are evaluated (Caswell 2001). Elasticity is defined as:

$$S_P = \frac{x_P - x_0}{x_0} \times 100 \qquad (13)$$

where S_P (%) is the elasticity of the output quantity to a given % increase in parameter P, x_0 is the output of the original model and x_P is the output of the model modified for parameter P (Barbeau & Caswell 1999, Lauzon-Guay et al. 2006). Elasticities of B^* (critical transition weight) and t^* (critical transition age) to independent perturbations of d_f, T_{fopt}, f_{opt}, p_1, a_2, b_2, p_2, d, T_{opt} and m_{opt} were calculated at 2 levels of parameter change, namely at 1 and 5%. To assess the influence of temperature, the analyses were repeated at 4 temperatures across the species thermal range, namely at 15, 20, 25 and 28°C for *Octopus ocellatus*, and at 13, 16, 18 and 21°C for *O. pallidus*.

RESULTS

Estimation of transition body mass and age

For both species, there was good agreement between the laboratory observations and the projec-

tions of the model (Table 3). Model estimates for B^* and t^* for *Octopus ocellatus* were close to the observed values (Table 3), encompassed within the 95% CI at 20°C and just outside the 95% CI at 25°C. *O. pallidus* did not display a 2-phase growth pattern during the 143 d of the experiment and the model predicted that exponential growth would always be supported at the temperatures tested (Table 3). Hence, only results for *O. ocellatus* are presented for the remaining analyses.

Impact of temperature on growth pattern

The relationships between temperature and threshold size and between temperature and threshold age were not linear. As temperature increases, B^* is projected to slowly increase while t^* is projected to decrease, so that the transition out of exponential growth would occur at an earlier age but similar body mass (Fig. 5). Beyond 25°C, however, B^* and t^* are both projected to increase so that the transition from exponential growth would be expected to occur later and at higher body mass.

Projected growth trajectories suggested that higher temperatures do not necessarily translate to higher body mass, with individuals growing at 23°C reaching higher body mass at 100 d than those at 28°C (Fig. 6). Projections at temperatures between 23 and 26°C produced the largest individuals. A 1°C change in environmental temperature produced a 1 to 15.5% difference in B^* and 0.1 to 16.2% in t^*, which resulted in a 0.7 to 62.6% difference in body mass at the end of the simulation. Simulation at 13°C suggested that exponential growth would always be sustained in the first 100 d.

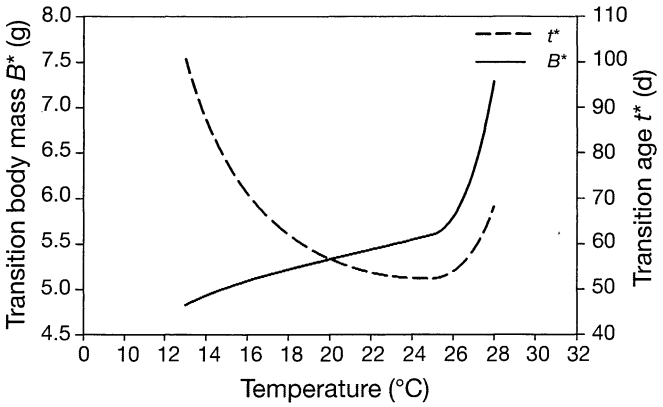

Fig. 5. *Octopus ocellatus*. Model threshold body mass B^* and transition age t^* as a function of environmental temperature T

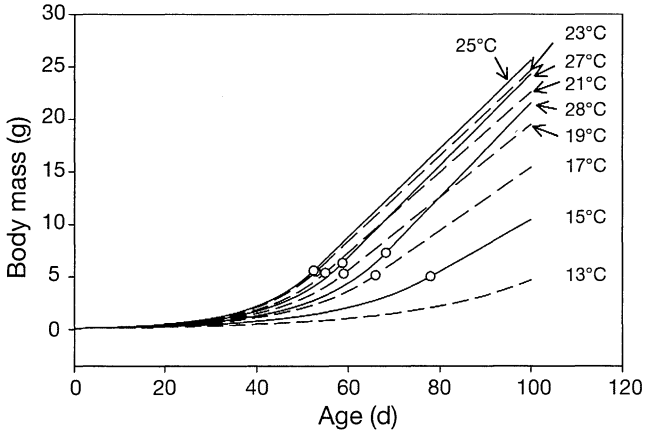

Fig. 6. *Octopus ocellatus*. Projected growth trajectories at selected environmental temperatures. (O): transition point (t^*, B^*) for each individual

Model sensitivity

Results from the sensitivity analyses performed with either ±1% or ±5% parameter changes were similar and hence for conciseness only the sensitivity analyses for a 1% increase are presented (Fig. 7).

The threshold body mass B^* was most sensitive to increases imposed on metabolic rate parameters, in particular to changes in b_2 and a_2. The corresponding transition age t^* exhibited a similar sensitivity profile. Temperature had the most effect on the sensitivity of B^* to changes in the feeding parameter T_{fopt} and growth parameter T_{opt}. The sensitivity of B^* to changes in metabolic parameters (and most feeding parameters) also increased with temperature, and was more pronounced at temperatures in the upper thermal range of the species. The sensitivity profile of transition age t^* was similar to that of B^* but was less influenced by temperature.

Table 3. *Octopus ocellatus* and *O. pallidus*. Comparison of observed (obs.) with simulated (sim.) threshold body mass B^* and transition age t^*. nt: no threshold

Species	Temp. (°C)	B^* obs. ± 95% CI (g)	B^* sim. (g)	t^* obs. ± 95% CI (d)	t^* sim. (d)
O. ocellatus	20.0	2.5 ± 3.5	5.3	43 ± 27	56.6
	25.0	2.3 ± 1.6	5.6	37 ± 12	52.4
O. pallidus	14.7	nt	nt	nt	nt
	16.9	nt	nt	nt	nt

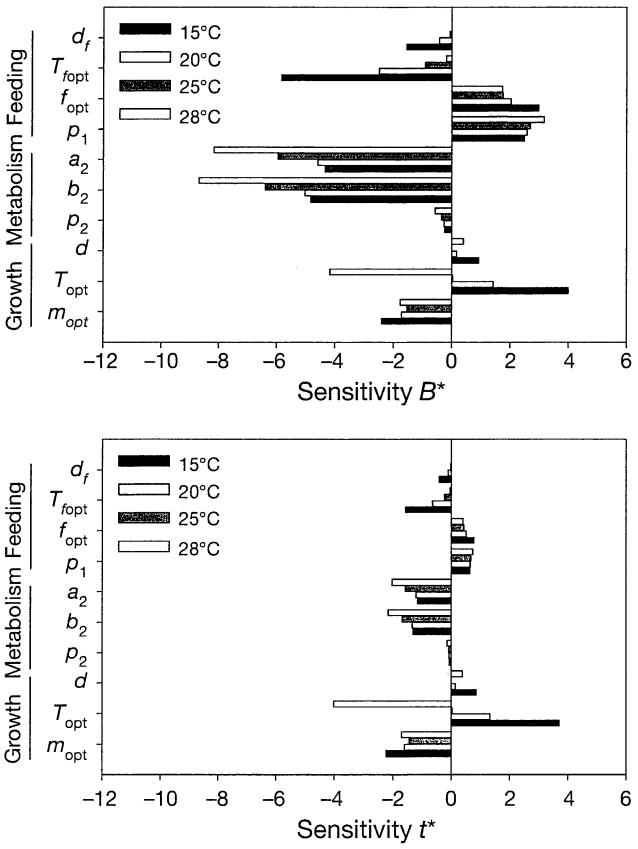

Fig. 7. *Octopus ocellatus*. Sensitivity to small perturbations in feeding, metabolism and growth rate parameters of (a) B^* and (b) t^* at 15, 20, 25 and 28°C. Elasticity was measured as the proportional change in B^* (body mass threshold size) or t^* (age at threshold size) resulting from a 1% increase in each parameter value

DISCUSSION

The energy balance paradigm reflected appropriately the conditions experienced by the animals and the growth pattern of both species, providing realistic estimations of the transition mass B^* and transition age t^* when 2-phase growth was detected experimentally. Results reinforce the hypothesis advanced by Forsythe (1993) that changes in environmental temperature as small as 1°C can have significant effect on cephalopod growth. A 1°C increase in temperature in the model implied up to 15.5% change in the threshold body mass for *Octopus ocellatus* and considerably altered the growth trajectory of individuals.

The model suggests that the influence of temperature on threshold body mass B^*, and hence on the shape of individual growth curves, would be mostly driven by metabolism. Sensitivity analyses indicate metabolic rate is the most influential component of the model and will generally more acutely influence threshold body mass rather than threshold age, as reported for *Sepia apama* with the basic energy balance model (Grist & Jackson 2004). More significantly, our analysis suggests that elevated temperature would increase the sensitivity of B^* to changes in metabolic rate, which would have important ramifications on the structure of cephalopod populations in the coming decades. The predicted increase in seawater temperature combined with a reduction in seawater pH, due to increasing CO_2 levels in the oceans, will decrease the ability of cephalopods to bind oxygen for transport (Seibel & Fabry 2003), therefore altering metabolic rate at the individual level. This would impact on the body mass at transition out of exponential growth, possibly affecting size at maturity, and is likely to substantially alter the population dynamics of most cephalopod species.

The reversal in the decreasing trend of t^* observed in model projections at higher temperatures is connected to the optimal temperature for growth T_{opt}. As temperature increases beyond that point, more energy becomes available from food while overall energy expenditure starts to decrease due to a decline in growth rate, hence delaying both the threshold time and body mass, at least until the optimal temperature for feeding T_{fopt} is reached. The accurate estimation of T_{opt} and T_{fopt} is therefore crucial for these type of energetic models, but these data are sparse for octopus.

Currently, the lack of a complete range of data on feeding, metabolism and growth for cephalopod species is an impediment, and models such as the one presented here require drawing parameters from a wide range of species. The estimated transition point being just outside the 95% CI at 25°C for *Octopus ocellatus* reflects these unavoidable approximations, and there is a need for concerted efforts to conduct the full range of observations on some species well suited to studies in captivity and representative of major fished species. There is also a need to establish whether temperature affects the metabolic rate and feeding rate exponents p_1 and p_2 for more species than just *O. vulgaris* (Katsanevakis et al. 2005). These exponents are considered temperature-independent in our analysis, but one or both of these parameters could vary with temperature with implications for size or age at transition out of exponential growth.

Energetic information on wild cephalopods is notoriously difficult to obtain. Average growth rate (Pecl 2004, Leporati et al. 2008) and aspects of metabolism (O'Dor et al. 1994, Webber et al. 2000, O'Dor 2002, Aitken et al. 2005) have successfully been estimated for a few species, but feeding data remains largely inaccessible. Carefully conducted laboratory studies with animals fed ad libitum and subject to minimal human interaction, as was the case for *Octopus ocel-*

latus in the present study, are thought to be representative of feeding and growth rates of wild animals (Wells & Clarke 1996), and remain the only option to fully parameterise energetics models for wild cephalopods. Field studies may never elucidate whether or not cephalopods demonstrate a 2-phase growth pattern in the wild. Growth curves that adequately represent the behaviour of a population mean can very poorly describe the pattern followed by any individual in that population (Alford & Jackson 1993). Furthermore, while statolith (Jackson 1990) and stylet increment analyses (Doubleday et al. 2006, Leporati et al. 2008) provide insights into individual growth rate integrated over the life span, the lack of a relationship between increment width and daily growth rate (Jackson & Moltschaniwskyj 2001) renders the detection of a change in growth difficult and the re-construction of individual growth curves impossible (Arkhipkin 2005). The present study suggests that a transition out of exponential growth is not a compulsory phase, and it may occur late, as seen for *O. ocellatus* at lower temperatures, or not at all, as seen for *O. pallidus*.

The model presented in the present paper is the first to include both body size and temperature-dependence in the overall energy budget of cephalopods and is adaptable to both squid and cuttlefish species. The incorporation of periodic variation in temperature to simulate seasonal water temperature would allow the inclusion of the 'Forsythe effect' (Forsythe 1993, 2004) and provide a better representation of the individual growth trajectories that are followed in natural populations. Individual variability could also be incorporated as stochastic variations in initial hatching size, which is known to significantly influence growth trajectory during the exponential phase (Pecl et al. 2004, Leporati et al. 2007). Such a model would permit a more in-depth exploration of population dynamics in natural cephalopod populations with great potential for improving fishery management by predicting population structure under prospective food and temperature scenarios. On a wider scale, this type of analyses could be used to predict how climate change might affect key cephalopod species. The negative impact of increasing pH, linked to ocean warming, could be incorporated in the metabolism term of the energy balance equation, enabling predictions about population abundance and structure under different climate change scenarios. Moreover, these types of models have the capacity to predict optimum conditions for potentially competitive species and could be a powerful tool for understanding both the evolution of species and for predicting how climate change might affect species distribution.

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Appendix 1. Oxygen consumption of juvenile pale octopus *Octopus pallidus*

AIM

The dependence of metabolic rate M on body mass B is characterised by an allometric scaling law of the form $M = q_2 B^{p_2}$. The purpose of the experiment was to estimate the species' metabolic rate exponent p_2.

METHODS

We reared pale octopus *Octopus pallidus* hatchlings from eggs in 250 l stock tanks under fluorescent lighting replicating natural daylight (06:00 to 18:00 h light, 18:00 to 06:00 h dark), and measured the oxygen consumption of 2 juveniles on 3 occasions at age 94, 134 and 148 d. All measurements were taken between 10:00 and 15:00 h while the animals were in post-digestive conditions (at least 12 h after feeding). Animals were placed in individual 600 ml clear plastic respirometers and a gentle flow of oxygenated water was passed through the respirometer for a period of 1 h in order to acclimatise the octopuses before measurements were taken (Fig. A1a). Care was taken to ensure that no air bubbles were trapped in the chambers. The water used in the respirometers was the same as that from the rearing tanks and was filtered (10 µm) before entering the chambers (Fig. A1b). Respirometers were immersed in a controlled-temperature water bath to maintain a constant temperature of 18°C for the duration of the experiment. Five respirometers were set up for each temperature treatment (4 with octopus and 1 blank). Respirometers were attributed randomly to octopuses to avoid any bias. After the acclimatisation period, respirometers were sealed by closing both taps. To ensure complete homogeneity of the sample, water was slowly mixed with a clear stirrer for 20 s before each sampling. This manipulation did not seem to disturb the octopus, which did not display any colour changes, rapid movements or noticeable increase in ventilation.

Water was sampled through the outflow with a 20 ml syringe, ensuring that no air was drawn into the syringe. The outflow tap was opened and the plunger slowly pressed to expel water samples. The first 5 ml of water expelled was discarded as this corresponded to still water sitting in the outflow tube. The duration of the experiment was 180 min for the measurements at 94 d and 120 min for the measurements at 134 and 148 d. Water samples for oxygen analysis and temperature measurements were removed hourly. Oxygen concentration was determined using a modified Winkler titration method (Major et al. 1972, Crowley 1999). In the modified method, volume was scaled down to 20 ml and manganese sulphate solution and potassium iodide/sodium hydroxide solution were micropipetted directly into the syringe. Duplicate titrations were carried out for each sample (two 10 ml titrations). All volumes of water extracted during the experiment were recorded precisely to correct the subsequent oxygen concentrations for volume. Oxygen consumption rate was calculated in µl O_2 g octopus^{-1} h^{-1} and converted to kJ d^{-1}.

RESULTS AND CONCLUSION

Oxygen consumption rate in kJ d^{-1} was expressed as $M = 0.0546B^{0.8774}$ (Fig. A2) and we hence estimated p_2 at 0.88 for *Octopus pallidus*.

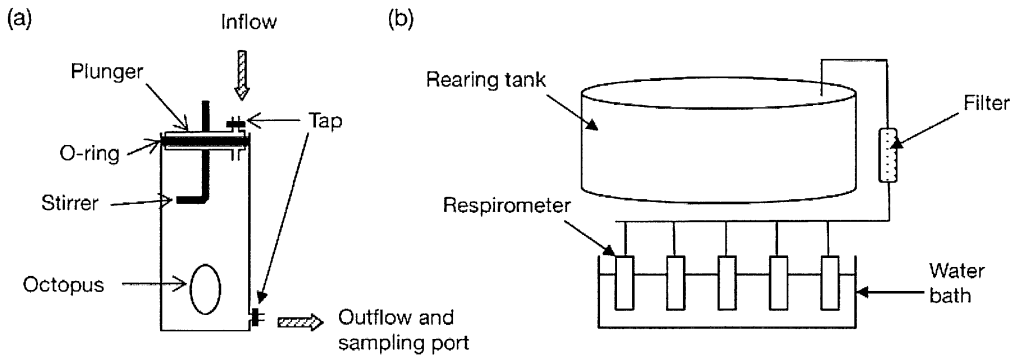

Fig. A1. (a) Respirometer design and (b) experimental setup for the oxygen consumption experiment

Appendix 1 (continued)

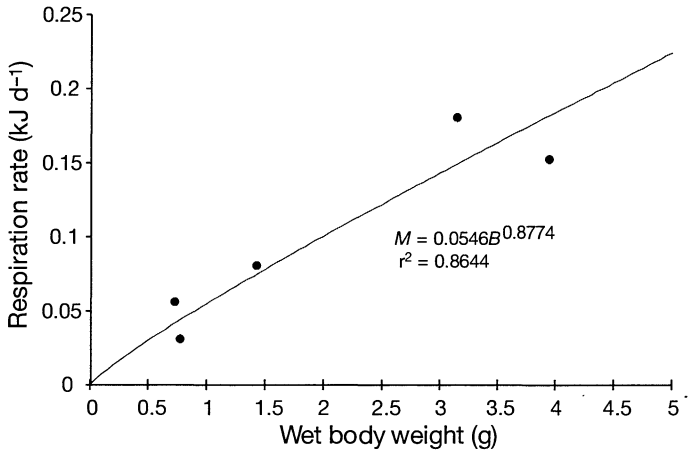

Fig. A2. *Octopus pallidus*. Oxygen consumption M as a function of body weight B for juvenile octopus at 18°C

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Modelling size-at-age in wild immature female octopus: a bioenergetics approach

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ABSTRACT: The population dynamics of cephalopods are poorly understood because intra-specific size-at-age is characteristically variable. Much of the variation observed is attributed to temperature and food, but other generally overlooked factors such as hatchling size and inherent growth capacities also affect size-at-age. In the present paper, we investigated the relative influence of the principal abiotic (environmental temperature) and biotic (food consumption, hatchling size, inherent growth capacity) factors affecting size-at-age in immature octopus. Using a bioenergetics model and size-at-age data of wild-caught immature *Octopus pallidus*, we simulated the juvenile growth trajectories of individuals hatched in different seasons (summer, autumn and winter) based on food availability, metabolism, environmental temperature and individual variability, under an assumption of 2-phase growth. Simulations predict that the effect of hatchling size on size-at-age was secondary to that of inherent growth capacity. Projections suggest that wild immature populations comprise a mixture of individuals displaying exponential growth and 2-phase growth and that the proportion of each depends primarily on the individuals' inherent growth capacities and food availability. High food intake was projected to decrease the number of individuals displaying 2-phase growth by delaying the transition between the 2 growth phases, resulting in larger individuals. Overall, individuals hatched in summer grew to larger sizes and matured earlier than individuals hatched in autumn or winter, independent of food availability. The size-at-age distribution of the summer and autumn cohorts tended to become bimodal under certain food intake levels, which highlights the importance of coupling size data with accurate age estimates in future octopus population studies.

KEY WORDS: Early life history · Energy balance · Individual-based model · Pale octopus

INTRODUCTION

Individual variability in growth has been observed in many taxa, including cephalopods (Domain et al. 2000), gastropods (Hughes & Roberts 1980) and teleosts (Searcy & Sponaugle 2000), resulting in intra-specific size-at-age data often being highly variable (Challier et al. 2006). Under these conditions, understanding population dynamics and changes in population size structure becomes challenging (Gurney & Veitch 2007), especially for exploited species. In cephalopods, growth rates are mainly governed by nutrition, body size, water temperature and, later in the life cycle, the energy diverted towards reproduction (Semmens et al. 2004). Both the quantity (Jackson & Moltschaniwskyj 2001, Villanueva et al. 2002) and quality (Segawa 1990, Iglesias et al. 2004) of food influence growth, with prey high in protein and low in lipid providing the highest growth rates (Segawa 1993, Lee 1994, García García & Aguado Giménez 2002). Water temperature is also of critical importance in defining cephalopod developmental rates, and there has been

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much emphasis on examining the effects of temperature on growth and its implications for size-at-age (see Forsythe & Van Heukelem 1987, Forsythe 2004; and Semmens et al. 2004 for a review). A key hypothesis that emerged from this research is the 'Forsythe effect' (Forsythe 1993, 2004), which states that when hatching occurs over a period of continually warming days (and hence warming water temperatures), each micro-cohort of hatchlings will grow significantly faster than micro-cohort(s) hatched only weeks previously. This hypothesis is supported by evidence from both laboratory (Villanueva 2000, Hatfield et al. 2001, Leporati et al. 2007) and field studies (Jackson et al. 1997, Hatfield 2000, Jackson & Moltschaniwskyj 2002), making seasonal temperature, along with nutrition, the 2 most important factors contributing to variations in size-at-age in natural populations.

Other generally overlooked factors, such as hatchling size (Pecl et al. 2004a, Leporati et al. 2007), can also affect size-at-age. Within a species, hatchling size is known to vary by at least 147% in squid (e.g. *Sepioteuthis australis*; Pecl et al. 2004a) and 239% in cuttlefish (e.g. *Sepia officinalis*; Domingues et al. 2001). Most cephalopods are believed to follow a 2-phase growth pattern, starting with a rapid exponential phase followed by a slower second growth phase, often represented by a power function (Semmens et al. 2004, Boyle & Rodhouse 2005). Given this growth pattern, differences between individuals at hatching can amplify throughout the lifespan (Pecl et al. 2004a) and have an impact on size-at-age. Hatchling size variation has multiple origins that can be divided into environmental effects, maternal effects and genetic effects. The direct effect of temperature on hatchling size is well known (Boletzky 1994), with higher incubation temperatures resulting in faster embryonic development and hence smaller hatchlings and, conversely, lower incubation temperatures resulting in slower development and larger hatchlings. Maternal condition during oogenesis can also introduce variation in intra-specific hatchling size, as hatchling size is positively correlated with maternal nutrition in several species (e.g. *Octopus vulgaris*; Sakaguchi et al. 2002 and *Euprymna tasmanica*; Steer et al. 2004). Genetic differences may also be a source of hatchling size variation. Multiple paternities within broods have been demonstrated for some cuttlefish (Naud et al. 2004) and squid (Shaw & Boyle 1997, Buresch et al. 2001) species, and difference in paternity has been linked to a difference in hatchling size (*Loligo forbesi*; Emery et al. 2001).

Another potential source of individual variability in size-at-age is inherent growth plasticity (Forsythe & Van Heukelem 1987, Boyle & von Boletzky 1996). Genotype is known to have a significant effect on physiological rates in molluscs, particularly on growth rate (Koehn 1991). Phenotypic plasticity, where a single genotype produces different phenotypes as a result of environmental conditions, also appears to play an important role in the variability observed in cephalopods (Boyle & von Boletzky 1996).

Different combinations of the above factors imply that size-at-age distributions for a given population can vary among micro-cohorts and years and, consequently, alter the overall population fecundity, which is largely determined by adult size in cephalopods (Mangold 1987). This is especially significant for species that have no overlapping generations and are commercially exploited, because population size and structure in any given year are direct functions of the success of breeding and recruitment from the previous year (Caddy 1983). This can lead to large inter-annual changes in abundance and render the population less likely to recover from overfishing, given the lack of multiple generations to compensate for low recruitment in any specific year.

Evaluating the relative influence of the many factors affecting size-at-age would require a precise knowledge of the various conditions experienced by individuals during their life history, such as quantity and quality of food consumed or the exact environmental temperatures experienced at each life stage. Obtaining this specific information for individual animals in the wild is difficult, and, although there has been progress with some species through tagging (Jackson et al. 2005), the low levels of tag retention, short life spans and high natural mortality reducing recapture rates remain problematic (Boyle & Rodhouse 2005). An increasing number of studies attempt to link the biology of cephalopods to their physical environment in nature (Lefkaditou et al. 2008, Pierce et al. 2008, Sanchez et al. 2008). Some studies have focused on growth and size-at-age in natural squid populations in relation to sea surface temperature (SST) (Hatfield 2000, Ichii et al. 2004, Pecl et al. 2004b), but, due to the lack of information, no other factors affecting size-at-age were taken into consideration. Controlled culture experiments provide some indication of the relative impact of different growth determinants (Forsythe & Hanlon 1988, Segawa & Nomoto 2002, Leporati et al. 2007) and remain invaluable to investigations of environmental influences on cephalopod life history. However, captivity can introduce biases and alter the actual processes of growth in cephalopods (Pecl & Moltschaniwskyj 1999). Moreover, changes in temperatures lead to large changes in growth rates and size-at-age (Forsythe et al. 2001, Hatfield et al. 2001), yet most experiments have used static temperature regimes that do not reflect the seasonal temperature variations encountered in nature.

The purpose of the present study was to use a modelling approach to investigate the relative influence of the principal abiotic (environmental temperature) and biotic factors (food consumption, hatching size, inherent growth capacity) affecting size-at-age in immature octopus. This method represents a complementary approach to both field and laboratory studies as it allows an investigation into the impact of factors such as food consumption in natural populations, which would otherwise not be possible. We generated an individual-based bioenergetics model, which determined the growth trajectories of individuals hatched in different seasons based on food availability, metabolism, environmental temperature and individual variability (i.e. hatchling size and inherent growth capacity). The model was parameterised with a combination of laboratory and field data and was validated against size-at-age data of wild individuals. We determined the level of individual variability in growth and food intake necessary to encompass the variation in size-at-age observed in our sample. We assessed the relative influence of individual variability and food availability on size-at-age, as well as the impact of food availability on the percentage of individuals displaying 2-phase growth and the age and size at the onset of sexual maturation. Our study species was the commercially exploited pale octopus *Octopus pallidus*, a temperate, medium-sized octopus (0.8 to 1.2 kg) with a 12 to 18 mo life span (Leporati et al. 2008b). Populations of this species show very little overlap in generations despite deposition of eggs all year round (Leporati et al. 2008b). Given that reproductive growth in octopus differs between sexes in both energy allocation and timing (Semmens et al. 2004), we chose, on the grounds of model parsimony, to limit our analysis to size-at-age in immature animals. In addition, as no immature males were caught during the 2 yr of sampling (Leporati et al. 2008a) upon which the present study was based, we focused the model on females only.

MATERIALS AND METHODS

Dataset. A total of 409 female *Octopus pallidus* were collected between 2004 and 2006 using a bottom set long line of octopus pots set at 26 m depth in Bass Strait waters, Tasmania, Australia (40° 43.342′ S, 145° 20.060′ E) (see Leporati et al. 2008a for details of the sampling regime). Individuals were weighed, aged via daily increments in the stylet (Leporati et al. 2008b), sexed and their reproductive status assessed (Leporati et al. 2008a). For the purpose of the present study, we selected all immature females hatched in January (n = 12), May (n = 12) and July (n = 18) 2005 to represent cohorts hatched in (austral) summer, autumn and winter, respectively. The dataset contained too few immature females hatched in spring 2005 for that seasonal cohort to be represented in our simulations. Gear selectivity and the large numbers of microcohorts within a year contributed to the low number of suitable data points. Given the high individual variability present in octopus, the sample sizes were nevertheless deemed sufficient to represent the range of size-at-age attainable in the wild.

Model development. The basis of the model was the temperature-dependent energy balance model (TEBM) described by André et al. (2009), which determines the shape and duration of the exponential growth phase in female octopus. The modified version presented here, the dynamic temperature-dependent energy balance model (DTEBM), allows the growth pattern of wild octopus hatched in different seasons to be simulated by adding the second growth phase, individual variability and dynamic temperatures to the original TEBM. Fig. 1 synthesizes the modelling approach used in the present study.

TEBM concept: The TEBM is based on the concept that cephalopod growth is bi-phasic and that energy conservation enforces the shift in growth between the 2 phases. The supply of energy E available to an individual depends on the balance between the energy

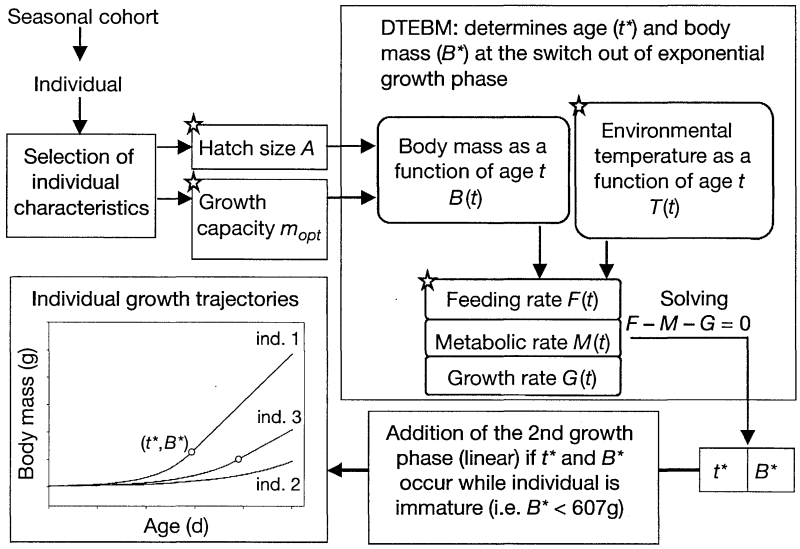

Fig. 1. Schematic representation of the modelling approach used to estimate individual growth trajectories. The purpose of the model was to investigate the relative influence of environmental temperature, food consumption, hatching size and inherent growth capacity (boxes marked with a star) on size-at-age in immature octopus *Octopus pallidus*

gained through food intake and the energy expended in metabolism and growth so that:

$$E = F - M - G \quad (1)$$

where F is the energy intake rate from food, M and G are the respective rates at which energy is expended in metabolism and somatic growth, respectively, and E must remain positive for the individual to survive. These rates are expressed in kilojoules per day in the present paper. Reproductive growth is not included here because we are concerned with immature individuals only. Grist & Jackson (2004) noted that all 3 terms on the right-hand side of Eq. (1) are dependent on body mass B, implying the possible existence of a threshold size B^* when $E = 0$. The feeding (F) and metabolic (M) rates traditionally follow an allometric scaling law of the form $Y = qB^p$ where $p > 0$ is a scaling exponent and $q > 0$ is a constant (West et al. 1997, Boyle & Rodhouse 2005, O'Dor et al. 2005). As growth is initially exponential, the initial growth rate G is directly proportional to body mass. All 3 rates are dependent on body mass B and environmental temperature T, and Eq. (1) can be re-expressed as:

$$\begin{aligned} E(B,T) &= F(B,T) - M(B,T) - G(B,T) \\ &= q_1(T)B^{p_1} - q_2(T)B^{p_2} - q_3(T)B \end{aligned} \quad (2)$$

where p_1 is the feeding exponent, p_2 the metabolic exponent and the functions $q_i(T)$ determine the temperature-dependency for the specific rate. Temperature dependency of feeding rate $q_1(T)$ and growth rate $q_3(T)$ were modelled with an inverted parabola to represent the general non-linear decrease in feeding and growth rates observed towards extreme temperatures (e.g. Ricker 1979, Mangold 1983, Bartsch 2002, André et al. 2009). This model has an optimum, corresponding to the maximum growth rate, and a symmetrical drop off on both sides (or asymmetrical if the optimum is not the midpoint of the species' temperature range). Assuming food is not a limiting factor, the temperature mediation of the growth rate is given by a symmetric inverted parabola:

$$q_3(T) = k_3 m(T) = k_3\left(m_{\mathrm{opt}} - h(T_{\mathrm{opt}} - T)^2\right) \quad (3)$$

where k_3 is the energy equivalent of octopus tissue, $m(T)$ is the growth rate coefficient, m_{opt} is the maximum value of $m(T)$ at the optimum temperature for growth T_{opt}, h is a constant and T is the ambient temperature. Similarly, the temperature mediation of the feeding rate is given by an asymmetric inverted parabola:

$$q_1(T) = \begin{cases} f_{\mathrm{opt}} - h_{f1}(T_{f\mathrm{opt}} - T)^2 & T < T_{f\mathrm{opt}} \\ f_{\mathrm{opt}} - h_{f2}(T_{f\mathrm{opt}} - T)^2 & T > T_{f\mathrm{opt}} \end{cases} \quad (4)$$

where $T_{f\mathrm{opt}}$ is the optimum temperature for maximum feeding rate f_{opt}, and h_{f1} and h_{f2} are constants. These equations represent the general case; it is worth noting that both feeding and growth rates may be improved at lower temperatures, for example, in areas subjected to upwelling (Jackson & Domeier 2003).

The temperature dependency of metabolic rate $q_2(T)$ is given by a modification of the Katsanevakis et al. (2005) equation:

$$q_2(T) = k_1 e^{\left(a_2 + \frac{b_2}{T + k_2}\right)} \quad (5)$$

where k_1 is the conversion factor from milligrams per hour to kilojoules per day, k_2 is the conversion factor from Kelvin to degrees Celsius, and a_2 and b_2 are constants.

When $E(B,T) = 0$ (Eq. 2), the individual reaches a threshold body mass B^* at a corresponding age t^*, after which it will no longer be able to cover its total energy expenditure rate. It is postulated that a shift from exponential growth to a slower growth phase is then enforced (Grist & Jackson 2004, 2007).

DTEBM and the estimation of the exponential growth phase: Whereas the TEBM describes growth at a fixed temperature, the DTEBM incorporates temperature dependence, which enables growth to be described under a seasonally fluctuating temperature environment (see Table 1 for description and values of DTEBM terms). We used a standard sinusoidal temperature function:

$$T = T_0 + T_1 \cos k(t + t_{\mathrm{hatch}} + c) \quad (6)$$

to represent seasonal environmental temperature T as a function of time of the year $(t + t_{\mathrm{hatch}})$, where t is the age of the individual (in days), t_{hatch} is the hatching day in a 365 d year, T_0 is the mean annual temperature (baseline), T_1 is the annual fluctuation of temperature around T_0 (amplitude), k is the frequency and c is the time lag necessary to align the maximum of the curve to the occurrence of the maximum temperature in a year (shift). Temperature parameters were determined from SST data for the years 2005/2006; the data were downloaded from the National Oceanic and Atmospheric Administration (NOAA) web site (www.noaa.gov).

Body mass is traditionally expressed as:

$$B(t) = Ae^{mt} \quad (7)$$

where t is the post-hatch age, A is the hatchling size and m is the fixed growth rate (d^{-1}). However, the growth rate coefficient m in this model is temperature dependent, so that body mass is now given by (see Appendix 1 for details of the calculation):

$$B(t) = Ae^{I(t)}$$

$$\text{where} \quad I(t) = \int m(t)\,dt \quad (8)$$

$$\text{and} \quad \begin{aligned} m(t) &= m_{\mathrm{opt}} - h(T_{\mathrm{opt}} - T)^2 \\ &= m_{\mathrm{opt}} - h\left(T_{\mathrm{opt}} - (T_0 + T_1 \cos k(t + t_{\mathrm{hatch}} + c))\right)^2 \end{aligned} \quad (9)$$

Table 1. Equations and parameter values for the dynamic temperature-dependent energy balance model (DTEBM). *A*: hatchling size; *t*: age (in days); t_{hatch}: hatching day in a 365 d year

Equations and parameters	Values
Growth rate *G*: $q_3(T)B$ with $q_3(T)$ from Eq. (3)	
Optimum temperature for growth (T_{opt}) (°C)	16.5
Growth rate coefficient at T_{opt} (m_{opt}) (d^{-1})	0.0217 to 0.0967
Parabolic constant (h)	5.14×10^{-4} to 2.3×10^{-3}
Energy equivalent of octopus tissue (k_3) (kJ g^{-1})	4.05848
Feeding rate *F*: $q_1(T)B^{p1}$ with $q_1(T)$ from Eq. (4)	
Optimum temperature for feeding (T_{fopt}) (°C)	18.4
Feeding rate at T_{fopt} (f_{opt}) (kJ d^{-1})	2.044
Parabolic constant if $T \leq T_{fopt}$ (h_{f1})	0.029
if $T > T_{fopt}$ (h_{f2})	0.0966
Feeding rate exponent (p_1)	0.75
Metabolic rate *M*: $q_2(T)B^{p2}$ with $q_2(T)$ from Eq. (5)	
Metabolic rate exponent (p_2)	0.88
Conversion factor (O_2 mg h^{-1}) to (kJ d^{-1}) (k_1)	0.33758
Conversion factor (K to °C) (k_2)	273.15
Constant (a_2)	21.80
Constant (b_2)	−6952.8
Temperature *T*: (Eq. 6)	
Baseline (T_0)	15.06
Amplitude (T_1)	2.83
Frequency (k)	2 × pi/365
Shift (c)	−73
Body mass *B*: (Eq. 8)	
$Ae^{\int m(t)dt}$	

By incorporation of $B(t)$ and $T(t)$ in Eq. (2), we obtain

$$E(t) = F(t) - M(t) - G(t)$$

where

$$\begin{aligned} F(t) &= q_1(T(t))B(t)^{p_1} \\ M(t) &= q_2(T(t))B(t)^{p_2} \\ G(t) &= q_3(T(t))B(t) \end{aligned} \quad (10)$$

The post-hatch age and body mass at which the exponential growth phase terminates in an individual were defined as t^* and B^*, respectively. Using Eq. (10), an iterative search was conducted for the threshold age t^*, which achieves $E(t) = 0$.

The corresponding body mass B^* was calculated according to

$$B^* = B(t^*) = Ae^{I(t^*)} \quad (11)$$

where

$$I(t^*) = \int_0^{t^*} m(t)dt$$

Food consumption in wild octopus. We evaluated average food consumption in captive *Octopus pallidus* on a crab diet (André et al. 2009) and estimated the parameters for the feeding rate $F(t) = q_1(t)B^{p_1}$. The optimum temperature for maximum feeding T_{fopt} was estimated at 18.4°C for this species. The corresponding f_{opt} was estimated at 0.584 (kJ d^{-1}) and the feeding rate exponent p_1 at 1.17. Specimens reared in the laboratory are held in an impoverished environment with limited food choice, tactile and visual stimuli, as well as restricted space. These factors may lead to suboptimal feeding (Houlihan et al. 1998), and it is reasonable to assume that the f_{opt} value would be higher in the wild. Moreover, a value of $p_1 > 1$ signifies that individuals always have enough energy intake to cover growth and metabolic costs, which is unlikely to be the case for animals in nature. A range of f_{opt} and p_1 values were therefore tested to identify plausible estimates for wild animals. For p_1, we explored a range of values from 0.40 to 1 in 0.05 increments, based on the lowest p_1 value of 0.39 described for an octopus species (*Octopus ocellatus*; André et al. 2009). For f_{opt}, we tested values up to 4 times the f_{opt} value found in the laboratory, corresponding to a range of values from 0.584 to 2.336 in increments of 0.292. Values >2.336 (kJ d^{-1}), equivalent to a food consumption in excess of 1 g crab flesh d^{-1} (according to values of O'Dor & Wells 1987) for a 0.3 g hatchling, were deemed too high for juveniles of this species.

Individual variability. We introduced individual variability at 2 levels: (1) variation in hatchling size (parameter A in Eq. 7) and (2) variation in inherent growth capacities (parameter m_{opt} in Eq. 9). We assumed that variation in inherent growth capacity and variation in hatchling size acted independently.

Hatchling size varies both within a cohort (intra-cohort variation) and between seasons (inter-cohort variation) (Pecl et al. 2004a). The model was parameterised with 3 seasonal distributions, namely summer, autumn and winter distributions for hatchling size, from which individuals were randomly selected. To do this, we first estimated the population variability in hatchling size from data obtained for 58 individuals hatched in winter (June) 2005 from a single brood originating from Bass Strait waters and maintained at ambient temperature in the laboratory (Leporati et al. 2007). The June hatchling distribution approximately

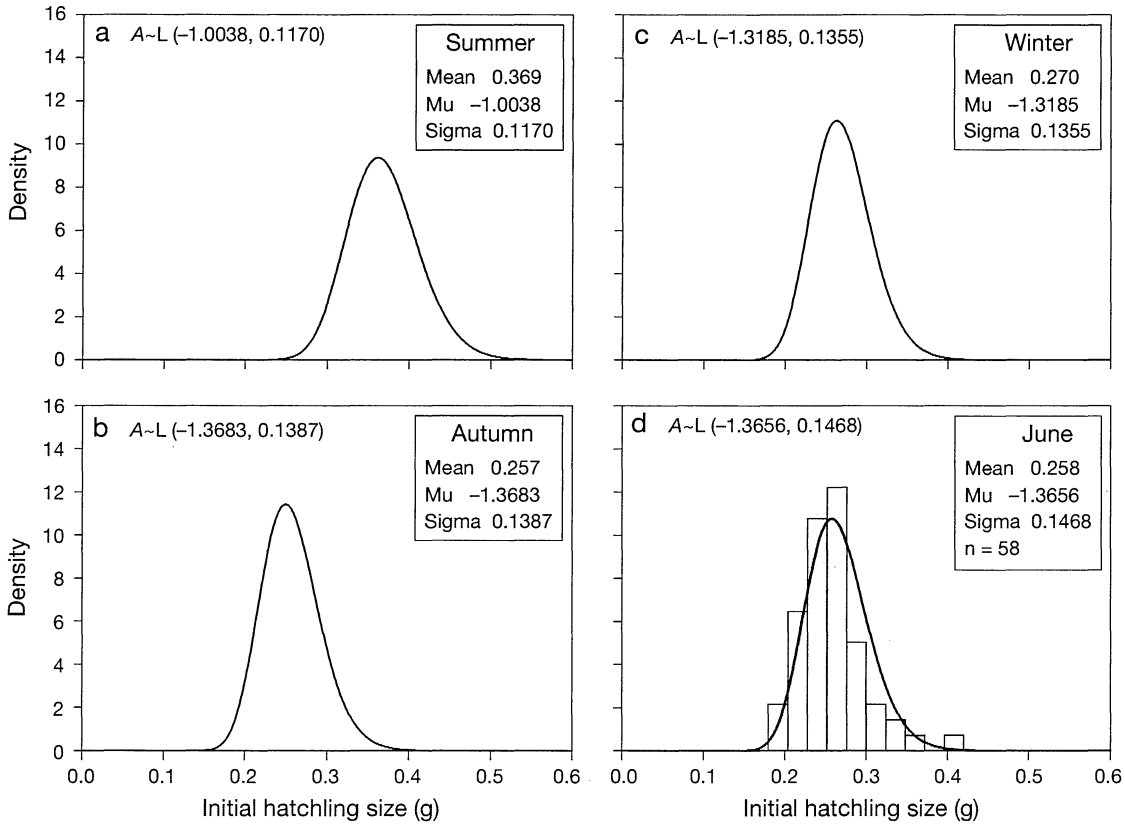

Fig. 2. *Octopus pallidus*. Hatchling size (*A*) selected from a log-normal distribution (L) defined by mu and sigma for: (a) summer, (b) autumn and (c) winter. Distributions were estimated statistically (see 'Materials and methods' section). (d) Estimated and observed June hatchling size distribution

followed a log-normal distribution (Fig. 2d) and was used as a template for the summer, autumn and winter seasonal hatchling size distributions (Fig. 2a to c), based on the following assumptions:

- The mean of the hatching size distribution is a function of incubation duration.
- While incubation duration in days varies with environmental temperature (Boletzky 1994), incubation duration in degree-days remains constant independent of the season. Incubation in degree-days (*incubdd*) was calculated according to:

$$incubdd = \sum_{1}^{incubdays} (dailytemp - T_{null}) \quad (12)$$

where *incubdays* is the observed number of days of incubation for the June cohort, *dailytemp* is the daily temperature and T_{null} is the threshold development temperature for *Octopus pallidus* eggs. Based on a threshold development temperature of 8°C, an observed *incubdays* of 150 d and known environmental temperature records from both Bass Strait (NOAA) and the laboratory, we estimated the incubation period to be 1067.5 degree-days.

- The relationship between the mean of the initial hatchling size distributions and incubation time (in days) is positively linear (Fig. 3a). Based on the incubation duration in degree-days, and assuming hatching on the first day of the month, we calculated the incubation duration (in days) for each monthly cohort using NOAA temperatures from the Bass Strait region (Table 2). We assumed the mean of the June hatchling size distribution to be that of our experimental brood (i.e. 0.258 g) and the proportional change in mean hatchling size to be 0.5% d^{-1} of additional incubation. This was based on an observed change in hatchling size of 25% for a 48 d difference in incubation duration between the summer and autumn cohorts in *Sepiotheuthis australis* (Pecl et al. 2004a), a species with a similar thermal range and hatchling size.
- The relationship between mean and variance of the initial hatchling size distributions is positively linear (Fig. 3b).

Inherent individual variability (both genotypic and phenotypic) was incorporated into the model via the parameter m_{opt} by assigning a specific 'growth potential' to each individual during the first (exponential) phase of growth before the start of the simulation. Values for the parameter m_{opt} were randomly

Table 2. *Octopus pallidus*. Predicted incubation time in Bass Strait waters (based on an incubation duration of 1067.5 degree-days) and mean of the hatchling size distribution. Asterisk represents observed data for pale octopus

Hatch month	Incubation (d)	Mean hatchling size (g)
Jan	197	0.369
Feb	181	0.347
Mar	148	0.303
Apr	122	0.268
May	114	0.257
Jun	115	0.258*
Jul	124	0.270
Aug	137	0.288
Sep	154	0.311
Oct	171	0.334
Nov	186	0.354
Dec	196	0.367

selected from a uniform distribution $m_{opt} \sim U$ (min_m_{opt}, max_m_{opt}), resulting in a different growth rate coefficient $m(t)$ for each individual (Fig. 4). As an initial estimate, we set the lower limit of the uniform distribution min_m_{opt} to 0.0167 (d^{-1}), corresponding to the m_{opt} value observed for *Octopus pallidus* in the laboratory at 16.5°C (André et al. 2009), and the upper limit max_m_{opt} to 0.098 (d^{-1}), corresponding to highest published growth rate for an octopus species in its exponential growth phase (*Octopus burryi*; Forsythe & Hanlon 1985), so that $m_{opt} \approx U(0.0167, 0.098)$. We varied the min_$m_{opt}$ and max_m_{opt} in 0.005 increments, so that min_m_{opt} = {0.0167, 0.027, 0.0267, 0.0317, 0.0367} and max_m_{opt} = {0.073, 0.078, 0.083, 0.088, 0.093}, and used the resulting uniform distributions to find a value pair (min_m_{opt}, max_m_{opt}) that reflected the data most accurately in the simulated projection.

Second slower growth phase. In *Octopus pallidus*, the sub-adult/adult growth phase does not appear to be influenced by temperature and seems to be exponential in form, although slower than the first exponential phase (Hoyle 2002, Semmens et al. 2004). There is, however, no information on the gradient of change in exponential growth between the phases of growth. Therefore, for model parsimony, we represented the second growth phase as linear and tangential to the transition point (t^*, B^*), as employed in Grist & Jackson (2007) (Fig. 5).

Sexual maturation. The onset of sexual maturation appears to be dictated by body mass rather than age in the pale octopus, with the mass at 50% maturity estimated for wild females at 472 g (Leporati et al. 2008a). However, the age and body mass at sexual maturity also depend on the food available to an individual (Mangold 1987), although the form of the relationship is not well defined. Given the lack of information on food consumption and its relation to sexual maturity in wild animals, we asserted that the body mass of the largest immature female found in the sampling year from which our data were extracted (i.e. 2005) would be the maximum body mass achievable by a juvenile in that specific year (i.e. 607 g). We therefore used 607 g as the body mass at which sexual maturity is achieved in our model (Fig. 5).

Other model assumptions. The following model assumptions were also made:

(1) Potential differences in activity levels are not taken into consideration; therefore, there is no individual variability in oxygen consumption rate other than that produced by differences in environmental temperature and body mass (i.e. individuals the same size and experiencing the same temperature regime will have identical oxygen consumption rates).

(2) All individuals within a micro-cohort have the same diet (crab) and have access to the same level of

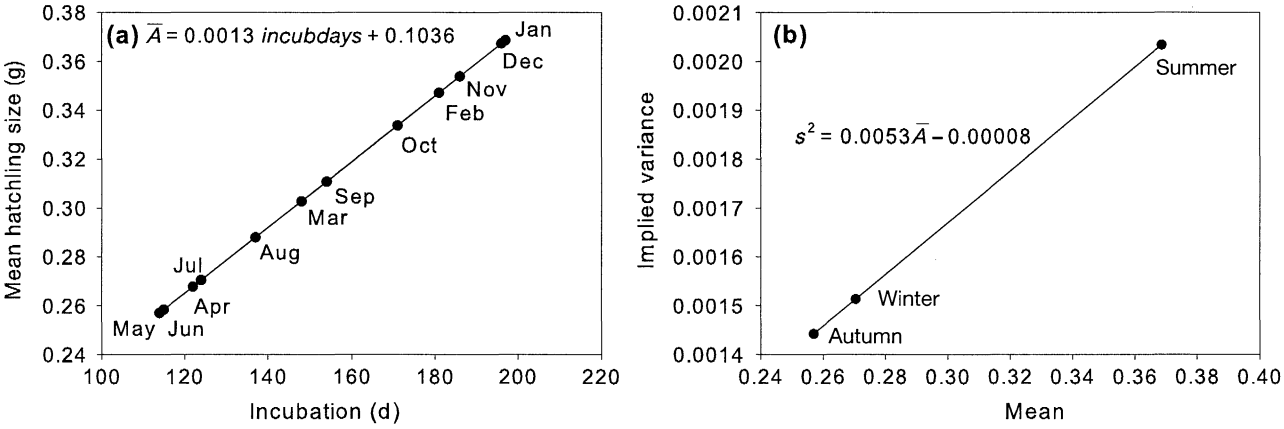

Fig. 3. *Octopus pallidus*. Estimation of seasonal hatchling size distribution parameters: (a) relationship between incubation time (*incubdays*) and mean of the hatchling size distribution ($\bar{A}$) and (b) relationship between mean hatchling size ($\bar{A}$) and variance (s^2) used to estimate the summer, autumn and winter hatchling size distributions

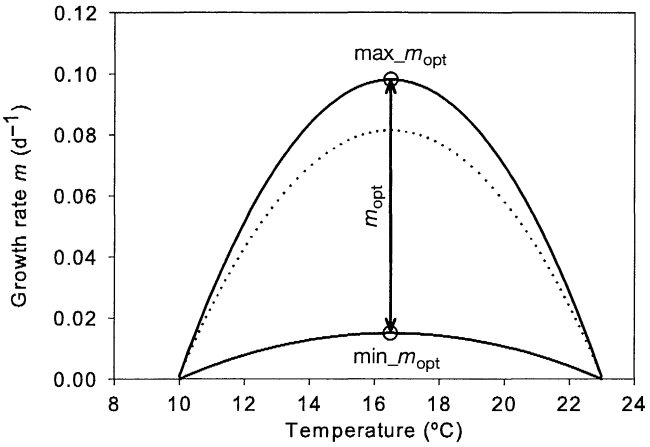

Fig. 4. *Octopus pallidus*. Plot of the exponential growth rate coefficient m as a function of temperature T. Inverted parabolic curves of the form $y = m_{opt} - h(T_{opt} - T)^2$ were used to describe $m(T)$. Inherent growth capacity was represented in the model by randomly selecting an m_{opt} value from a uniform distribution U(min_m_{opt}, max_m_{opt}) and assigning the resulting $m(T)$ curve (e.g. dotted line) to each hatchling at the start of the simulation

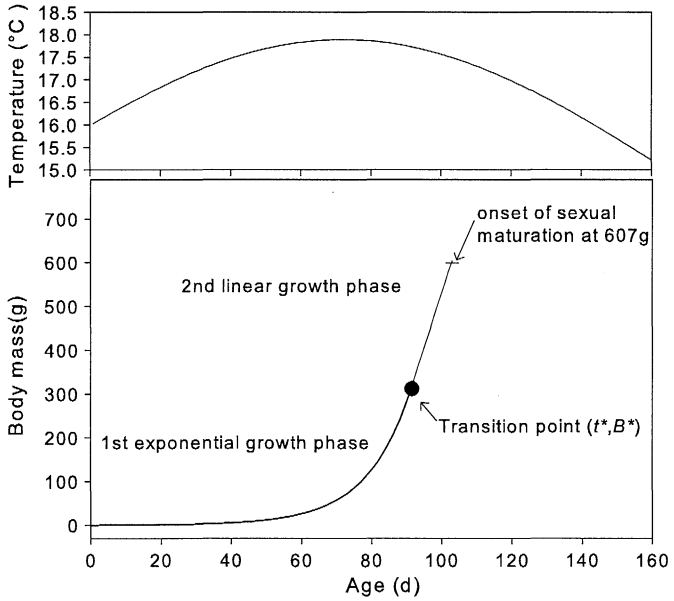

Fig. 5. *Octopus pallidus*. Plot of the projected individual growth trajectory (here a 2-phase growth pattern) of a summer-hatched individual parameterised with an initial hatchling size A = 0.194 g, optimum growth rate m_{opt} = 0.083 d^{-1} and optimum feeding rate f_{opt} = 1.49 kJ d^{-1}

food. Hence, there is no individual variability in food consumption other than that produced by differences in environmental temperature and body mass.

(3) As octopus are opportunistic predators, there is no inter-seasonal variation in food consumption (i.e. the feeding parameters remain the same independent of season).

Simulation. We simulated 3 seasonal micro-cohorts, each containing 200 individuals, which were started on 1 January (summer cohort), 1 May (autumn cohort) and 1 July (winter cohort) 2005. Individual juvenile growth trajectories within each micro-cohort were projected up to a body mass of 607 g, corresponding to the assumed size at maturity. Simulations were aimed at investigating the influence of environmental temperature, food consumption, hatchling size and inherent growth capacity on size-at-age. Juvenile mortality was not taken into consideration in the projections.

The model was first tuned by adjusting the feeding constant f_{opt}, the feeding exponent p_1 and the range of possible optimum growth rates (min_m_{opt}, max_m_{opt}), until the size-at-age data observed in wild ocotopus were contained within the 5th to 95th percentile range of size-at-age produced by the model for each season.

We then investigated the influence of seasonal temperature on size-at-age for each micro-cohort from projections of the body mass distributions of immature individuals. As the age of the youngest mature individual in each of our seasonal samples varied between 3.75 and 5 mo, we projected size-at-age up to 4 mo of age (namely at 60, 90 and 120 d) in order to include as many immature simulated individuals as possible in our analyses. The relative influence of individual variability in hatchling size and in inherent growth capacity on the simulations were determined independently, by randomising the respective parameters A or m_{opt}, whilst holding the other parameter constant either at the mean m_{opt} or the mean value of hatchling size A (i.e. randomised A with fixed m_{opt} or randomised m_{opt} with fixed A). We investigated the influence of food availability by altering the f_{opt} value from 0.584 to 2.336 (kJ d^{-1}) in increments of 0.292 (corresponding to 1.5–4 times the f_{opt} value estimated for laboratory animals), and then assessing the impact on size-at-age, the proportion of individuals displaying 2-phase growth and age at 50% sexual maturity (estimated here as the age at which 50% of the individuals have reached 607 g).

RESULTS

Estimation of growth and feeding parameters for wild-caught octopus

An m_{opt} range of 0.0217 to 0.0967 (d^{-1}) was necessary to encompass all the variability observed in our sample of wild-caught octopus, and we subsequently used the distribution $m_{opt} = U(0.0217, 0.0967)$ for the rest of the analyses. While other feeding parameter combinations provided acceptable model fits under the selected m_{opt} range, the combination of 0.75 (p_1) and 2.044 (f_{opt}) pro-

vided the most plausible representation of the predicted size-at-age, which tightly surrounded the available data (Fig. 6). This combination was used to explore predicted size-at-age at 60, 90 and 120 d and the age at sexual maturity in our sample.

An f_{opt} value of 0.584 was deemed improbable under natural conditions as it resulted in unrealistically slow growth of individuals. This f_{opt} value was removed from subsequent analyses, so that only the range from 0.876 to 2.336 was used to estimate the influence of food intake on size-at-age and age at sexual maturity.

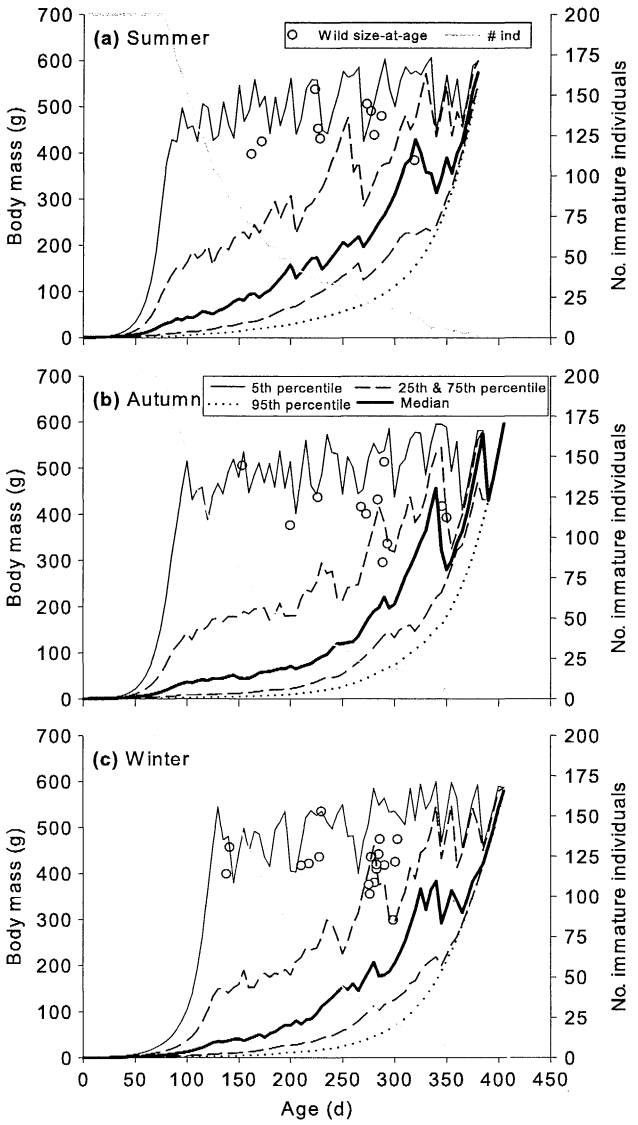

Fig. 6. *Octopus pallidus*. Simulated size-at-age (with both optimum growth rate m_{opt} and hatchling size A randomised) for immature octopus (n = 200) hatched in: (a) summer, (b) autumn and (c) winter. Thin solid lines: 5th percentile; dotted lines: 95th percentile; dashed lines: 25th and 75th percentile; thick solid lines: median; solid grey lines: number of immature individuals left in the model; circles: size-at-age data of wild individuals from the Bass Strait fishery

Projected size-at-age at 60, 90 and 120 d

Size-at-age within a cohort was extremely variable (Fig. 7), with an up to 435-fold difference between the smallest and largest individuals at 120 d. Variability increased with time in all seasons, but the range of possible sizes attained was smaller for the winter cohort up to 90 d (2.4 to 579 g for summer cohort, 1.4 to 570 g for autumn cohort and 0.8 to 119 g for winter cohort). Individuals hatched in summer consistently grew faster and reached a larger size than those hatched in other sea-

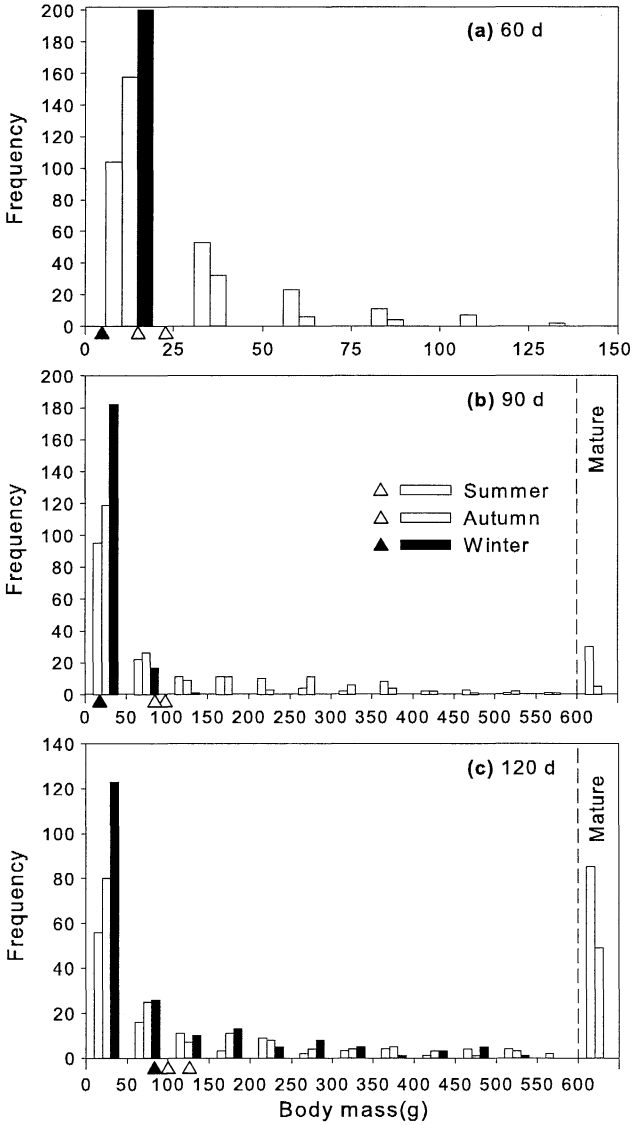

Fig. 7. *Octopus pallidus*. Simulated body mass distributions (with both optimum growth rate m_{opt} and hatchling size A randomised) for summer-, autumn- and winter-hatched octopus (n = 200) at: (a) 60, (b) 90 and (c) 120 d. Seasonal mean body mass values are represented by triangles. Note the different scale for the x-axis in (a). Also, note that at 90 and 120 d, some individuals in the summer and autumn simulations had already reached maturity (607 g)

sons. The autumn cohort was the second fastest growing cohort and presented a similar size-at-age distribution to summer-hatched individuals. At 120 d, 42% of the summer-hatched individuals had reached 607 g, compared to 24.5% of the autumn-hatched individuals, and were removed from the projection. Winter-hatched individuals presented the smallest size-at-age distribution of the 3 seasons, reaching only 2/3 of the size of their summer counterparts at 120 d (mean body mass: 83.9 g (n = 200) for the winter cohort and 126.3 g (n = 116) for the summer cohort).

Projected age at sexual maturity

The onset of sexual maturity, represented by a drop in the cohort's median body mass as the first individuals reached 607 g and 'moved out' of the model, differed between seasons. Summer-hatched individuals reached sexual maturity earlier than individuals hatched in other seasons, with maturation starting at 80 d for the first individual and 50% maturation being reached at 130 d. Although there was little difference in the age at 50% maturity between autumn- and winter-hatched individuals (175 vs. 180 d, respectively), maturation started earlier in autumn-hatched individuals, with the first individuals starting maturity at 90 d compared to 125 d for the winter-hatched cohort.

Relative influence of hatchling size and inherent growth capacity on size-at-age

Hatchling size produced an up to 2-fold difference in size-at-age, but generated less variation than inherent growth capacities independent of hatch season (Fig. 8). The size-at-age variation observed in our sample of wild-caught octopus was not encompassed by either inherent growth capacity or by hatchling size variation alone for the summer cohort.

Projected influence of food intake on size-at-age

The 3 cohorts presented slightly different patterns with regards to the influence of food availability on size-at-age. For all cohorts, increased food availability resulted in larger individuals, with a range of sizes from 0 to 350 g in summer and 0 to 100 g in autumn and winter for an f_{opt} of 0.876, compared to 0–600 g for all seasons for an f_{opt} of 2.336 (Fig. 9c,f,i). The impact of food availability, however, only became apparent at 3 mo of age for the summer and autumn cohorts and at 6 mo of age for the winter cohort, with earlier size-at-age distributions being almost identical and independent of f_{opt}. Summer and autumn cohorts also became bi-modal at 120 d under certain food intake levels, namely f_{opt} = 0.876 and 1.168 for summer and f_{opt} = 1.168 and 1.46 for autumn (Fig. 9c,f).

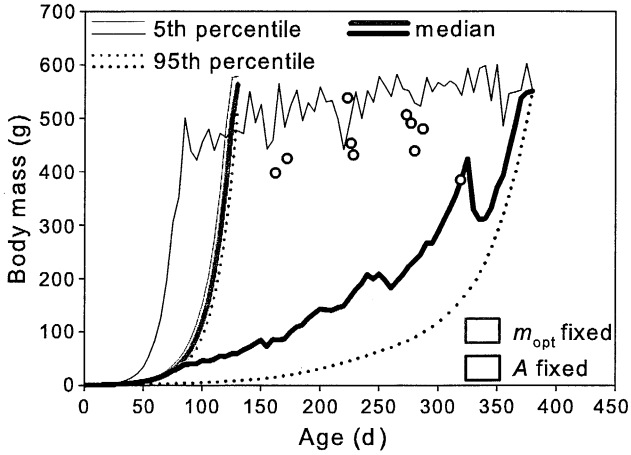

Fig. 8. *Octopus pallidus*. Simulated size-at-age for immature octopus (n = 200) hatched in summer. The relative influence of individual variability was investigated by fixing hatchling size and randomising growth capacity (*A* fixed model, black lines) and by fixing inherent growth capacity and randomising hatchling size (m_{opt} fixed model, grey lines). Thin solid lines: 5th percentile; dotted lines: 95th percentile; thick solid lines: median; circles: size-at-age data of wild individuals from the Bass Strait fishery. The simulated size-at-age for the autumn and winter cohorts encompassed all the size-at-age data of wild individuals and were not presented here for conciseness

Higher food availability also resulted in a lower proportion of individuals displaying 2-phase growth within each cohort (Table 3). An optimum feeding rate f_{opt} of 2.336 kJ d^{-1} enabled between 87 and 100% of all individuals to grow exponentially for the entire duration of their juvenile phase depending on the hatching season, whereas f_{opt} values of 0.876 kJ d^{-1} forced between 74.5 and 89% of all individuals to display 2-phase growth.

Projected influence of food intake on age at sexual maturity

Increased food availability (up to f_{opt} = 1.46 kJ d^{-1} for the summer and autumn cohorts and f_{opt} = 1.752 kJ d^{-1} for the winter cohort) resulted in earlier sexual maturation, bringing the age at maturity forward by 5 d to 5.8 mo. Higher levels of food intake had little or no impact on the age of maturity (Table 3, Fig. 9c,f). Summer-hatched individuals consistently matured earlier independent of the feeding rate, reaching maturity between 45 and 205 d before individuals from other cohorts.

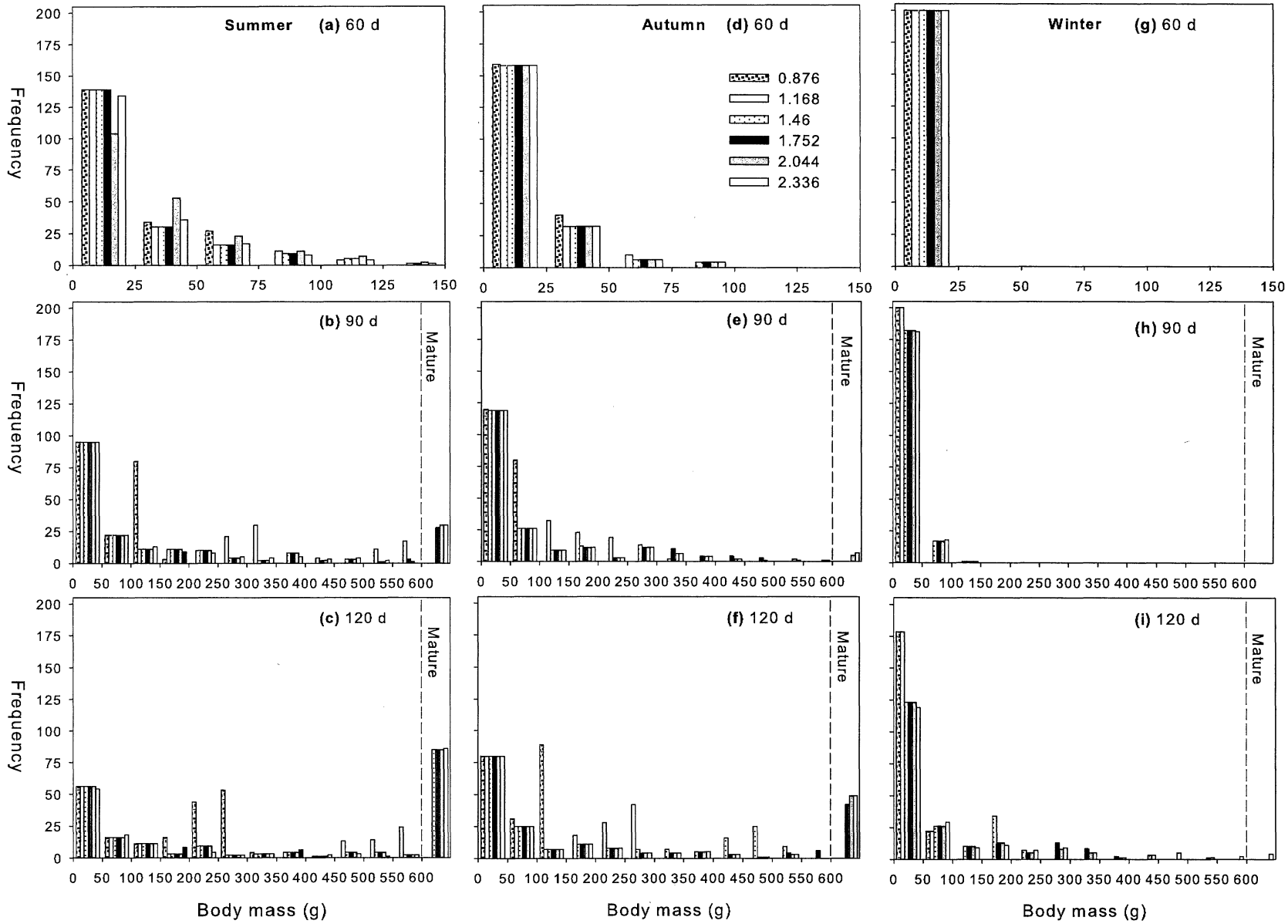

Fig. 9. *Octopus pallidus*. Simulated body mass distributions (with both optimum growth rate m_{opt} and hatchling size A randomised) of 200 summer-hatched (a,b,c), autumn-hatched (d,e,f) and winter-hatched (g,h,i) *octopus* at 60, 90 and 120 d under various food availability (f_{opt} = 0.876 to 2.336). Note that (a,d,g) are on different scales. Also note that at 90 and 120 d, some individuals in the summer and autumn simulations had already reached maturity (607 g)

Table 3. *Octopus pallidus*. Influence of food availability (expressed as f_{opt}) on the percentage of octopus displaying 2-phase growth and on the age at which 50% of the cohort reached maturity (50% mat.) for summer-, autumn- and winter-hatched cohorts. A 30 d difference in age at 50% maturity was considered significant

f_{opt}	Summer		Autumn		Winter	
(kJ d^{-1})	2-phase (%)	Age 50% mat. (d)	2-phase (%)	Age 50% mat. (d)	2-phase (%)	Age 50% mat. (d)
0.876	89	195	79.5	350	74.5	340
1.168	63.5	135	65	210	59	340
1.460	36	130	53	175	45	195
1.752	14	130	39.5	175	30.5	180
2.044	0	130	23.5	175	16.5	180
2.336	0	130	12.5	175	10.5	180

DISCUSSION

Food availability has a major impact on size-at-age and age at sexual maturity. Overall, increased food availability results in larger individuals, which is consistent with observations from laboratory experiments on octopus species including *Octopus tetricus* (Joll 1977), *O. ocellatus* (Segawa & Nomoto 2002) and *O. vulgaris* (Villanueva et al. 2002). The present model suggests that high levels of food intake in the early life stage delays the switch to a slower growth phase, enabling individuals to grow exponentially for longer periods and reach larger sizes in a shorter time period. While this is evident for the summer and autumn cohorts, the winter cohort appears unaffected by food availability in the first 3 mo after hatching. Due to their slow growth rates as a response to low water temperatures, individuals from the winter cohort are able to maintain exponential growth for longer time periods, and only a few experienced a transition in growth phase in the first 90 d post-hatching. Similarly, the apparent lack of influence of food intake on size-at-age in the first 2 mo for the summer and autumn cohorts is linked to the timing of the transition in growth phase. Only very low food intake (e.g. f_{opt} = 0.876) enforces a switch in growth rates in the first 60 d post-hatching, while other food levels lead to changes at 3 mo of age, or beyond.

High levels of food intake also resulted in earlier sexual maturation in our simulations, which is concordant with previous observations on captive octopus (*Eledone moschata*; Boletzky 1975) and cuttlefish (*Sepia officinalis*; Boletzky 1979). As the onset of sexual maturity is related to size in *Octopus pallidus* (Leporati et al. 2008a), individuals with high food consumption grow faster and therefore reach the body size at which sexual maturity occurs earlier, independent of the season.

Inherent growth capacities had a strong influence on size-at-age. Growth rates necessary to encompass all the variation in the wild size-at-age sample were substantially higher than growth rates obtained in captivity (Leporati et al. 2007, André et al. 2009), with an average m_{opt} value for wild individuals of 0.0592 compared to 0.0167 under laboratory conditions (André et al. 2009). Captivity can alter growth in cephalopods (Joll 1977, Pecl & Moltschaniwskyj 1999), so higher growth rates in wild individuals are likely. Alternatively, low growth rates comparable to those obtained in captivity may be characteristic of some hatchlings from natural populations, but these small, slow-growing individuals may be unlikely to recruit to the fishery due to size-selective mortality in early life history (Conover & Schultz 1997, Steer et al. 2003) and gear selectivity of fisheries pots (minimum catch size = 250 g). The observation that all the wild size-at-age data, independent of season, were encompassed within the 5th and 50th percentile range of size-at-age produced by the model results from the lack of small specimens (<250 g) in our dataset due to gear selectivity.

Although secondary to the effect of inherent growth capacity, variations in initial hatchling size still influenced growth. The impact of hatchling size is, however, likely to be underestimated, as the hatchling size distribution used in the present study was estimated from 1 brood only, which possibly under-represents the real range of hatchling sizes in the wild for this species.

Simulation results agreed with the Forsythe effect, i.e. during the period of decreasing temperatures, individuals grew slower, and cohorts that hatched earlier grew larger than subsequent cohorts hatched in cooler conditions. The summer cohort was overall the fastest growing cohort as a result of a combination of larger hatchling size, caused by longer incubation periods over winter and spring, and elevated water temperatures in the first months post-hatching. Autumn and winter hatchling size distributions were nearly identical due to similar incubation periods, but the autumn cohort benefited from warmer water temperatures and, hence, faster growth rates.

There has been extensive debate over the existence of a 2-phase growth pattern in wild populations of cephalopods, although this is often observed in captivity (Domain et al. 2000, Jackson & Moltschaniwskyj 2002, Semmens et al. 2004, Arkhipkin & Roa-Ureta 2005, Boyle & Rodhouse 2005). Model simulations suggest that the population comprises a mixture of individuals displaying exponential growth only and 2-phase growth and that the proportion of each grouping depends primarily on the individuals' inherent growth

capacities and food availability. Low food intake and/or high inherent growth capacity lead to an increase in the proportion of individuals displaying 2-phase growth, as animals cannot sustain exponential growth for long periods under these conditions. However, even at the lowest food consumption in our simulations, some individuals never displayed 2-phase growth and between 11% (summer cohort) and 25.5% (winter cohort) of the individuals in each cohort maintained exponential growth throughout their immature stage. These individuals had low inherent growth capacities, which enabled them to maintain low growth rates. High food consumption ($1.752 < f_{opt} < 2.336$ kJ d^{-1}) also led to an absence of 2-phase growth in the summer cohort during the juvenile phase, with all individuals displaying exponential growth. While being the most 'successful', the summer cohort was also the most sensitive to changes in food availability, with proportionally more individuals switching from exponential only to 2-phase growth as f_{opt} decreased. Considering the levels of individual variability in the factors influencing the timing of the transition between the 2 growth phases, i.e. food consumption, inherent growth capacity, and also variations in metabolic rates due to activity and specific dynamic action (which were not included in this model), it is likely that the fraction of the juvenile population displaying 2-phase growth in nature would be variable at any given time. Detecting the existence of a 2-phase growth pattern in a wild population through typical sampling would be very difficult, if not impossible, as growth curves that adequately represent the average behaviour of a population can very poorly describe the pattern followed by any individual in that population (Alford & Jackson 1993). Detection of 2-phase growth may be achieved through an intensive mark-and-recapture program in a natural semi-enclosed area (Van Heukelem 1976). Another possibility would be to explore whether growth increments in stylets correlate with growth rate, in which case 2-phase growth could be detected for wild octopus.

The impact of maturity on the shape of individual growth curves is unclear. The additional energetic demands associated with reproduction may enforce the shift to a slower growth phase in individuals that have maintained exponential growth during their juvenile phase, and may impose further reductions in growth rates in individuals that have already shifted out of exponential growth. In any case, the progression of the size-at-age distribution in mature individuals is likely to be different from that seen in immature individuals.

The present study highlights the importance of coupling size and age data for any population study on cephalopods. Using size data alone to investigate the dynamics of wild populations could be misleading, as the size distribution of the summer and autumn cohorts tends to become bimodal with time under certain levels of food availability. While this phenomenon is in effect a consequence of the size difference between individuals that are still in exponential growth versus those that have already switched to a slower growth phase, this bimodality in size distribution could be misinterpreted as being 2 separate cohorts. This is especially relevant to octopus population studies that have traditionally used modal progression analysis on length-frequency data (*Octopus mimus*, Cortez et al. 1999; *Eledone cirrhosa*, Relini et al. 2006) for low-cost fisheries assessment, due to the lack of an aging method for these cephalopods. Recent technical developments based on stylet (an internal remnant 'shell' unique to octopus) increment analyses now allow aging in octopods (Doubleday et al. 2006, Leporati et al. 2008b), and the current study highlights the importance of accurate age estimates in future population studies.

While encompassing many factors relevant to size-at-age in wild populations, the simulations presented here are still simplistic compared to situations in nature. Larger sample sizes would provide a better estimation of individual variability in the wild and, together with improvements to the metabolic rate term (with inclusion of the energy expended in movement and in post-prandial activity), would produce more precise growth predictions at the individual level. The assumption of constant food consumption independent of seasons may not be accurate either, as food quality and quantity are known to fluctuate seasonally. However, cephalopods are generalists that appear unselective in their choice of prey (Mather 1993, Boyle & Rodhouse 2005) and are, therefore, likely to find sufficient food all year round, although periods of lower food availability might involve an increase in the energy expended in foraging activities. The simulations nevertheless provide some new insights into growth processes in wild benthic octopus. The shape of the growth curve (and hence size-at-age) is not only strongly influenced by seasonal temperatures during the early post-hatch phase, but also by seasonal temperatures during incubation. While the later may not be as relevant to species with short incubation periods, such as many squid species or merobenthic octopus species (producing 1000s of planktonic hatchlings, e.g. *Octopus vulgaris*), seasonal temperatures during incubation can result in large differences in size at hatching for species with incubation extending over the time frame of a season (e.g. *O. pallidus*). In the context of the predicted warming of the oceans, we can expect some significant changes in the seasonal size-at-age distribution of many octopus species. Shorter incubation periods due to higher water temperatures, com-

bined with changes in temperature regimes post-hatching and increased variation in food availability, could lead to modifications of the population structure and possibly a change in reproduction strategy, for example shifting from a year round reproductive pattern to a more seasonal pattern.

As for many cephalopod species, the lack of information on early life stages is problematic when attempting to model their life cycle. In order to refine our understanding of population structure and dynamics, future studies should focus on obtaining size-at-age information for individuals prior to their recruitment to the fishery (i.e. <250 g for *Octopus pallidus*), as well as specific information on hatchling size distribution, which is critically lacking for cephalopod species.

Cephalopod population dynamics are complex due to the short life spans and fast responses to environmental conditions of these highly plastic animals. The present study has shown the relative influences of the combined, and sometimes counteractive, biotic and abiotic factors on cephalopod growth. Quantifying inherent growth plasticity in octopus is possible, and any reasonable attempt to model population dynamics in these species should include in some form or another seasonal temperatures, food availability and individual variations.

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Appendix 1. Calculation of body mass (B) under a seasonally fluctuating temperature environment. T: temperature; m: growth rate coefficient; t_{hatch}: hatching day in a 365-day year; T_0: baseline; T_1: amplitude; k: frequency, c: shift

In the dynamic temperature-dependent energy balance model (DTEBM), the individual growth rate in the first phase of growth is given by:

$$\frac{dB}{dt} = m(T(t))B \quad \text{(A1)}$$

where $T(t) = T_0 + T_1 \cos k(t + t_{hatch} + c)$. Eq. (A1) must therefore be solved to obtain body mass as a function of individual post-hatch age t. Integrating left and right sides of Eq. (A1):

$$\ln B + a = \int \left(\frac{1}{B}\right) dB = \int m(T(t))dt \quad \text{(A2)}$$

where a is a constant determined by initial hatch mass, so that after rearrangement:

$$B(t) = Ae^{I(t)} \quad \text{(A3)}$$

where A is the initial hatch mass and $I(t) = \int m(T(t))dt$.

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